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*American Philosophical Society
1919, Classified List of members.*



American Philosophical Society

(Founded 1727)

By direction of the Officers and Council the accompanying classified list of members is sent to you so that after its perusal you may suggest nominees for membership in your department of learning, whom you think would be most fully entitled by their researches and qualifications for election into the Society.

Will you please forward to the Secretaries very promptly any names of persons whom you may desire to suggest so that they may be collated and considered in time to be available by January 12th next, for action at the annual election in April following, when, under the Laws, nominees not exceeding fifteen in number in any one year, may be elected to membership.

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PROCEEDINGS
OF THE
American Philosophical Society
HELD AT PHILADELPHIA
FOR
PROMOTING USEFUL KNOWLEDGE
VOLUME LVII
1918



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THE AMERICAN PHILOSOPHICAL SOCIETY
1918

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PROCEEDINGS
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American Philosophical Society
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The Archæological Significance of an Ancient Dune. By CHARLES C. ABBOTT . . .
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By VICTOR G. HEISER . . .



PHILADELPHIA
THE AMERICAN PHILOSOPHICAL SOCIETY
104 SOUTH FIFTH STREET
1918

American Philosophical Society

General Meeting—April 18-20, 1918

The Annual General Meeting of The American Philosophical Society will be held on April 18th, 19th, and 20th, 1918, beginning at 2 P. M. on Thursday, April 18th.

Members are requested to send to the Secretaries, at as early a date as practicable and before March 9, 1918, the titles of papers which they intend to present so that they may be announced in the *preliminary* programme which will be issued immediately after that date and which will give in detail the arrangements for the Meeting. It is understood that papers offered are original contributions which have not been theretofore presented.

The Publication Committee, under the rules of the Society, will arrange for the immediate publication of the papers presented in either the *Proceedings* or the *Transactions*, as may be designated.

I. MINIS HAYS
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Members who have not as yet sent their photographs to the Society will confer a favor by so doing; cabinet size preferred.

It is requested that all correspondence be addressed

TO THE SECRETARIES OF THE

AMERICAN PHILOSOPHICAL SOCIETY

104 SOUTH FIFTH STREET

PHILADELPHIA, U. S. A.

PROCEEDINGS
OF THE
AMERICAN PHILOSOPHICAL SOCIETY
HELD AT PHILADELPHIA
FOR PROMOTING USEFUL KNOWLEDGE

INTERRELATIONS OF THE FOSSIL FUELS.*

III.

By JOHN J. STEVENSON.

(Read November 2, 1917.)

THE JURASSIC AND TRIASSIC COALS.

THE JURASSIC.

Like the Cretaceous, this is barren in the greater part of its extent within Europe and the productive areas are of limited extent, though some of them are important. Conditions favoring accumulation of coal existed in widely separated localities elsewhere, as in Siberia, Australia, New Zealand and Alaska; in some of which the deposits may prove to be valuable. The geologic features have material bearing upon the problem under consideration in this study.

Great Britain.—British geologists have grouped the Jurassic deposits into Upper, Middle, Lower Oölite and the Lias. Transition from the Cretaceous is often gradual. Local deposits of coal are in the Lower Oölite and soils of vegetation have been observed in both the Upper and the Lower Oölite.

The Purbeck "Dirt Beds," soils of vegetation near top of the Upper Oölite, have been mentioned in most of the text-books on

* Part I. appeared in these *Proceedings*, Vol. LV., pp. 21-203; Part II., in Vol. LVI., pp. 53-151.

geology. They were described first by Webster, then by Buckland and de la Beche and still later by Mantell.¹ The chief "Dirt Bed" with erect stumps was recognized by all as a black loam with remains of tropical plants, which accumulated where they grew. This soil, about one foot thick, contains slightly rounded fragments of stone and, as Webster showed, is the original matrix of the silicified stems; for, wherever exposed, it contains trunks of coniferous trees, partly in the black earth and partly surrounded by the overlying calcareo-silicious strata. The intervals are very nearly the same as those seen in recent forests and the erect stumps or stools of the large trees with attached roots are in their original soil. Associated with the coniferous stems are others of cycad-like plants, also silicified. The same condition was observed at another locality, where the dip is 45 degrees and the stems are vertical to the plane of bedding.

Mantell states that the "Dirt Bed" has a considerable quantity of lignite and of waterworn pebbles. While the prevailing trees are conifers, there is abundance of plants allied to *Zamia* and *Cycas*. Many of the trees are erect, as if petrified during growth. The roots are in the black clay, and the stems reach into the overlying calcareous rocks. Just prior to Mantell's visit, a large area of the "Dirt Bed" has been exposed preparatory to removal that the underlying rock might be quarried. Some of the trunks were surrounded by calcareous earth; the upright stems were only a few feet apart and usually were not more than 3 or 4 feet high; without exception they are splintered at the top as though they had been wrenched or snapped off. All are without bark and have a weather-worn surface, resembling that of posts set between tides. Two other dirt beds were examined by Mantell, who obtained cycads from both: the principal bed is so little consolidated that he was able to dig out several cycads and to prove that they are actually *in situ*.

¹ T. Webster, "Observations on the Purbeck and Portland Beds," *Trans. Geol. Soc.*, II., Vol. 2, 1829, pp. 41, 42; W. Buckland and H. T. de la Beche, "On the Geology of the Neighborhood of Weymouth, etc.," the same, Vol. 4, 1836, pp. 13-15; G. A. Mantell, "Geological Excursions around the Isle of Wight," 3d ed., 1854, pp. 286-290.

The conditions described by Mantell recall those seen by Russell² on the Yahtse of Alaska. That stream, issuing as a swift current from beneath a glacier, invaded a forest area and surrounded the trees with sand and gravel. Some stems, still retaining their branches, projected above the mass but most of the decaying trunks had been broken off by the wind and entombed in prostrate position. The phenomenon is familiar to all who have travelled along rivers with broad bottoms. Lyell states that the top beds of the Portlandian or middle division of the Upper Oölite, containing marine shells, were covered with fluviatile muds on which *Zamia* and cycads grew.³ He remarks that each dirt bed may represent a notable period of time; 2 to 3 feet of vegetable soil is the only product of very old tropical forests.

The Kimmeridge Clay, at base of the Upper Oölite, contains, according to Phillips,⁴ a highly bituminous shale, which is utilized as fuel at Kimmeridge on the Purbeck coast. As shown in cliffs near that place, the clay, finely laminated and grayish-yellow, with remains of plants and animals, passes gradually into a bituminous shale, which is dark brown, lusterless, slightly calcareous and burns with a smoky flame. Lyell⁵ states that this sometimes becomes an impure coal and that in Wiltshire it resembles peat. Plant remains are rare and the bitumen may be due, at least in part, to animal matter.

The coal at Brora in Scotland belongs to the Great Oölite or highest division of the Lower Oölite, which in that region is a mass of sandstones and shales. The seams at Brora are thin, but one of them was worked many years ago for local use. This petty area was described by Murchison, whose measurements are (1) fossil shells, marine, quartz grains, carbonaceous matter, all cemented by calcareous material, passing downward into a mass of compressed leaves and stems, in turn becoming shaly coal, 2 feet, 7 inches; (2) coal resembling jet, divided midway by a parting of pyritous, in-

² I. C. Russell, "Second Expedition to Mount St. Elias," 13th Ann. Rep. U. S. Geol. Survey, 1893, Part I., p. 14, Pl. XII.

³ C. Lyell, "Elements of Geology," 6th ed., New York, 1866, pp. 391-393.

⁴ J. Phillips, "Outlines of Geology of England and Wales," Part I., 1822, pp. 127, 128.

⁵ C. Lyell, "Elements," p. 394.

durated clay; in burning it gives off the characteristic odor of imperfect coal; the powder is brown, 3 feet, 3 inches to 3 feet, 6 inches. This is one of the few localities in Britain where coal is present in workable thickness, but the coal is inferior and no longer of even local importance. Miller⁶ has given some notes concerning the Oölite conglomerate of Eigg, one of the Hebrides. The Scur of Eigg is described as a mass of igneous rock resting on a pile foundation, composed of pine stems, laid crosswise. These stems of *Pinites eiggensis* are transported material; they are so numerous near Helmsdale that the people collect them and burn them into lime. The tree was as abundant on the mainland of Scotland as the Scotch fir is at present. It was of slow growth but attained gigantic size. Witham's study of the structure proved it very different from that of the Carboniferous conifers. The wood abounds in turpentine vessels or lacunæ of varying size, which are well defined, the minutest detail of structure being distinct. Occasionally Miller found a thin streak of brilliant lignite, resembling that of Brora, but in every case it was only the bark of a tree.

The Lower Oölite in Lincolnshire, according to Morris,⁷ has soils of vegetation with well-defined underclays. In one section, bituminous clay, 18 inches thick, rests on "gray clay with vertical stems and roots descending from the overlying bed." Another section shows the bituminous band only 6 inches thick with 7 feet of underclays containing vertical stems. At Dane's Hill the root-bed is only 9 inches, but at Aunby Cutting, he saw two bituminous clays, of which the upper contains lignite and impure coal. Each has its root-bed below.

The Inferior Oölite, at base of the Lower Oölite, has some coal in Yorkshire. Phillips⁸ recognized two groups of sandstones and shales along the coast. The lower consists of white to yellow sandstones and shales, with irregular seams of bad coal; the plants are cycads and ferns but equisetiform remains are in the upper layers, standing vertically as if in place of growth. A thin irregular seam

⁶ H. Miller, "The Cruise of the *Betsy*," Boston, 1862, pp. 51-55, 71.

⁷ J. Morris, "On Some Sections in the Oölitic District of Lincolnshire," *Quart. Jour. Geol. Soc.*, Vol. 9, 1853, pp. 326-331.

⁸ J. Phillips, "Geology of Yorkshire," 2d ed., London, 1835, Part I., pp. 8-10, 65, 66, 173, 174.

of coal near the top has been mined at some places. The higher group contains thin irregular coal seams; one, 8 inches thick, rests on 4 feet of grit holding carbonaceous markings and at 80 feet lower a white sandstone, associated with coal, has similar "coal pipes." Coal seams are present throughout northeastern Yorkshire and occasionally become thick enough for mining, but the coal is not good. The flora consists preëminently of ferns, but cycads and conifers are abundant.

Fox-Strangways and Barrow⁹ have given additional details respecting the east coast of Yorkshire. A section on Gresthope Bay, where the Middle Estuarine Series of the Lower Oölite consists of thin-bedded sandstones and shales, shows (1) black coaly shale, 0 feet, 3 inches; (2) soft, white sandstone with rootlets, 1 foot; (3) gray shale, 5 feet; (4) sandstone and shale, 3 feet, 6 inches; (5) black shale, 1 foot, 6 inches; (6) fine laminated sandstone, 1 foot, 6 inches; (7) fine laminated shale, 6 feet; (8) false-bedded sandstone, with irregular patches of coal, plants, pyrite and carbonized wood, 21 feet. The last rests on the Millepore Series, in which rippled sandy shales occur; the impure coal at top of the section rests on the sandy floor into which the plants thrust their roots.

The Lower Estuarine series is exposed at many places between Whitby and Scarborough, where it underlies the Millepore Series. A section at Blea Wyke shows a thin coal seam roofed by 30 feet of dark shale and resting on 2 feet of underclay, below which is ferruginous sandstone, 12 feet, containing great numbers of erect stems, allied to *Equisetites* and often 5 feet high. Two other seams, 2 and 3 inches thick and separated by 2 feet of soft sandstone, are at 18 feet below the top seam. The lower one rests on 6 feet of dark shale overlying 24 feet of false-bedded sandstone. In the Hawsker District, a coal seam, 4 inches, is at only 3 feet above the Dogger and the intervening shale contains roots. The Dogger in this district has vertical stems of *Equisetites*. The Middle Estua-

⁹ C. Fox-Strangways, "The Geology of the Oölitic and Cretaceous Rocks South of Scarborough," Mem. Geol. Surv., 1880, p. 5; "The Geology of the Oölitic and Liassic Rocks to the North and West of Malton," Memoirs, 1881, p. 8; the same and G. Barrow, "The Geology of the Country between Whitby and Scarborough," 1882, pp. 31, 32.

rine Shale Series at Cloughton Wyke has vertical *Equisetites* in sandy shale and, at base, a false-bedded sandstone as in the area south from Scarborough.

Judd¹⁰ has given the section of a pit at Ufford, Northampton, in the Lower Estuarine sands, which shows a thin seam of lignite, below which are 3 feet of purplish clay and 3 feet of sand, both of which contain plant remains in vertical position; he considers that the manner of occurrence indicates that the plants are *in situ*, and that they were embedded by quiet deposition as they stood. Kendall¹¹ states as result of study of clays along the Yorkshire coast, that every coal seam examined by him rests on a root bed.

The resemblance of the Estuarine Series to the Carboniferous Coal Measures has been emphasized by several observers; the resemblance to those of the Cretaceous is equally marked. The deposits were laid down in shallow water at many horizons within the Oölite. Ramsay¹² and his associates observed that, in their district, there is much false-bedding in both the Great and the Inferior Oölite as well as in the Forest Marble, which has many fragmentary fossils in its sandy layers. Even the deposits containing marine forms frequently give evidence of deposition in shallow water. Scrope¹³ reported that many layers of the Forest Marble Beds (Great Oölite) in the neighborhood of Bath are rippled and that they show impressed footprints of various types. Those layers contain rolled fragments of shells, corals, echini, etc., and exhibit the characteristic features of a shore deposit. According to Lyell, rippled bands of Oölite are known in broad areas and are utilized for roofing.

The Lias of England is without coal, though at some localities jetified wood is abundant. The soils of vegetation in Yorkshire were described by Conybeare and Phillips:¹⁴ Conybeare stated that

¹⁰ J. W. Judd, "The Geology of Rutland," Mem. Geol. Survey, 1875, pp. 104, 105.

¹¹ P. F. Kendall, in letter of May 27, 1917.

¹² A. C. Ramsay, W. T. Aveline, E. Hull, "Geology of Parts of Wiltshire and Gloucestershire," Mem. Geol. Survey, 1858, pp. 10, 12, 14.

¹³ G. P. Scrope, "On the Rippled Markings of the Forest Marble Beds," *Proc. Geol. Soc.*, Vol. 1, 1834, p. 317.

¹⁴ W. D. Conybeare, "Outlines of the Geology of England and Wales," 1822, p. 272; J. Phillips, "Geology of Yorkshire," 1835, p. 66.

gigantic reeds are in the cliffs near High Whitby. They appear to have been rooted in a bed of shale or slate-clay and their remains protrude into a sandstone, 5 feet thick. Those which are erect retain their shape, but prostrate stems are compressed. The tops seem to have been broken off and the woody matter has disappeared, there being only sandstone casts. Phillips gave more of detail. He reports that a Lias sandstone near Whitby contains great numbers of cylindrical plants like *Equiseta*, which are erect. They were broken off above and in some cases do not reach to the top of the bed. They are broken off below but commonly pass to the lower surface of the bed and, at times, the lower joints reach into the underlying shale. The conditions have led some to regard these plants as *in situ*, but Phillips prefers to believe that they were floated down and that they were kept vertical by the weight of their roots. The writer is compelled to dissent from this explanation. If the trees had been floated down stream, they would not remain vertical, even though it be conceded that the weight of their roots would keep them vertical while floating. As soon as the roots had touched bottom, the current, gentle or strong, would push the stem down stream. "Snags," only too familiar in our western rivers, invariably point down stream. Grand' Eury was able to determine the direction of currents in St. Etienne coal basin by means of "snags" enclosed in the sandstones. Murchison,¹⁵ in a brief note referring to the observations by Phillips, stated that he had discovered another locality at the same horizon, but 40 miles away and well inland. At both localities, the stems of *Equisetum columnare* are in the normal position and appear to be rooted in the black shale. The only fossil accompanying these plants is a fresh-water bivalve.

France.—The Jurassic deposits of France contain some thin seams of coal, which rarely have more than local importance. de Serres¹⁶ reported upon the coals of Aveyron, belonging to the Lower Oölite. The mines are on the plateau of Larzac within an area of

¹⁵ R. I. Murchison, "On the Occurrence of Stems of Fossil Plants in Vertical Position, etc.," *Proc. Geol. Soc.*, Vol. I, 1834, p. 391.

¹⁶ M. de Serres, "Des houilles sèches ou stipites des terrains jurassiques, etc.," *Bull. Soc. Geol. France*, t. 16, 1859, pp. 97-99, 104, 105.

not more than 60 by 200 kilometers. The only workable seam is extremely variable. The greatest thickness is in the group of mines known as Nuejols, where the seam is 70 to 80 centimeters. The center of the area is on the summit of the plateau, where, in two mines, the thickness is but 45 centimeters. The decrease continues toward the north, there being only 12 to 15 centimeters at 10 kilometers north from La Cavalerie. The lower part of the coal group is largely calcareous and the limestones have both marine and freshwater forms. The coal rests directly on black shale; the roof is similar but more carbonaceous and, at times, has a wood-like structure; it is at most 12 centimeters thick and is combustible. The coal yields a very fair coke with imperfect metallic luster. The lenticular form of the seam is distinct, for the thickness decreases in all directions from La Cavalerie.

Austria.—The Jurassic coals of Upper Austria belong to the Grestener beds at the base of the Lias. They have been described by Lipold¹⁷ and his associates. Hertle, in his notes upon the mining area of Bernreuth on the eastern side of this region, states that Czjžek's profile shows a marine limestone between two coal seams, which contains *Mytilus*, *Pleuromya* and *Pecten*, and a sandy shale in the same section has *Ammonites*. Sphærosiderite concretions as large as half a cubic foot are fossiliferous. These calcareous deposits were not exposed at the time when Hertle made his examination, but he saw a sandy shale with *Pholadomya* and *Mytilus*. The coal seam, which is mined, is 3 feet thick and rests on an underclay containing remains of plants. The coal looks like good coal but it has 42 per cent. of ash.

Near Gresten, according to Rachoy, the coal seams are in a sandstone group. One tunnel cut seven streaks of coal, one to 12 inches thick, while a shaft passed through 16 seams, 3 inches to 3 feet thick. The roof and floor are sometimes clay and sometimes sandstone. The thickest bed yielded a good caking coal with less than 4 per cent. of ash; the dip is about 20 degrees. Plant remains are poorly preserved but marine fossils occur in fine condition. At

¹⁷ M. V. Lipold, G. v. Sternbach, J. Rachoy and L. Hertle, "Das Kohlengebiet in den nördlichen Alpen," *Jahrb. k. k. Geol. Reichsanst.*, Band 15, 1865, pp. 29-61.

Hinterholz, Rachoy found dips of 40 to 60 degrees and one seam, 4 feet 6 inches thick, was mined. The coal yielded 66.3 per cent. of high-grade coke, used in iron-making.

v. Sternbach's section near Grossau is (1) shale, 6 inches; (2) coal and shale, 1 foot; (3) clay shale, 1 foot; (4) coal, 3 feet; (5) shale, 6 inches; (6) sandstone, 6 feet; (7) carbonaceous shale, 6 inches; (8) coal, 6 inches; (9) carbonaceous shale, 6 inches; (10) sandstone, 1 foot; (11) shale, not measured. This, like many others, closely resembles typical short sections in Cretaceous and Carboniferous coal measures. The workable seam, Number 4, has lenses of shale, so that not more than three fourths of the output is clean coal. The roof is black shale but the floor is fine to coarse sandstone. The dip is from 55 to 60 degrees and the coal seams are extremely variable; but the variations seem to be due only in part to serious disturbance. In the Pechgraben area, v. Sternbach saw 6 well-defined coal seams as well as numerous streaks of coal in the great Franz-Stollen, where the dip is 40 to 50 degrees and the rocks as well as the coal are much shattered. The sandstones have been broken into great wedges, which interlock with similar wedges of shale. The coal seams are thin and often are distorted; but they show variations, which clearly are not due to disturbance of the stratification. The third seam, where first opened at the outcrop, consisted of numerous streaks, one to 3 inches thick; it was prospected for a considerable distance in the hope that these streaks would unite; eventually the mass became 4 feet thick but about one half of the shale still remained. The sixth seam is 9 feet thick in the tunnel, where it has 5 clay partings, in all 3 feet. But this seam, resting on shale with plant remains, is variable; in another tunnel the thickest seam is only 16 inches, while in another it is from 3 inches to 2 feet. One cannot determine in the strongly disturbed area whether the seams are lenticular or not, but there are considerable areas, in which according to the diagrams, there was little disturbance and the succession is normal; in these the lens-form is distinct. The coal is somewhat inferior, having 17.2 per cent. of ash. This Pechgraben coal, according to v. Gümbel,¹⁸ shows woody

¹⁸ C. W. v. Gümbel, "Beiträge, etc.," 1881, p. 160.

structure distinctly after treatment with Schultze's solution; even the minute details can be recognized.

The whole region of the Lias, except locally, is much disturbed, dips of 80 degrees being by no means rare, but the coal throughout contains a high percentage of volatile combustible matter and yields a strong coke. The Grestener deposits are very largely sandstone. No freshwater fossils were noted by any of the observers but there is abundant evidence of repeated invasions by the sea; the marine mollusks belong to off-shore types.

Hungary.—The importance of Liassic coals in Austria, where land conditions became pronounced, prepares one for the great development farther east in Hungary. The coal-bearing formation belongs to the Lower Lias and, according to Hantken,¹⁹ the coals are as important to Hungary as the Carboniferous coals are to England, Belgium, France and Germany, the seams being thick and the coal good. There are five important districts: Doman-Resicza, Steierdorf-Anina, Berszaszka, Fünfkirchen-Uralja and Neustadt-Törzburg; the first three are in the Krassoer Comitatus between 39 and 40 degrees of Longitude and between 44 and 45 degrees of North Latitude and are near the Serbian border; the fourth is near the 36th meridian and the 46th parallel, while the fifth is in Transylvania, close to the border of Roumania.

In the Doman-Resicza district the Lias rests on deposits of Dyas age and the dip is from 30 to 90 degrees, at times overturned. Two seams, 40 meters apart, are intercalated in the sandstone mass. The thickness of each is from nothing to nearly 3 meters and the variation is as marked along the strike as along the dip. Each has clay as floor and roof, so that the coal is apt to be dirty.

The Lias sandstone in the Steierdorf-Anina district rests on Dyas. It is 160 meters thick, light in color, is almost clean quartz sand with some mica and little clay or cementing material. There is about 10 meters of other rock, including the coal seams. These thicknesses, according to Hantken, are averages only, for all portions of the section, especially the coal seams, are variable. Eleven coal horizons were seen, of which 5 have workable seams, one to 4

¹⁹ M. Hantken, "Die Kohlenflöze, etc., der Ungarischen Krone," Budapest, 1878, pp. 44-118.

meters thick. Immediately above the lowest seam is a laminated sandstone, carbonaceous and containing many plants of swamp types. The upper part of this sandstone, floor to the second seam, is somewhat argillaceous and holds vertical plant remains resembling roots. The coal seams consist ordinarily of several benches, some of them good, but others worthless. Kudernatch's section at one locality shows (1) upper bench, clean coal, 0.713; (2) earthy, impure coal, a mixture of Faser and bright coal, locally known as "Brand," 0.552; (3) middle bench, clean coal, 1.025; (4) coal and shaly coal, 0.053; (5) lower bench, clean coal, 1.394; (6) impure coal, not mined, has steel-like luster, 0.154; total, 3.891 meters. The coal is in bright and dull laminæ, but the bright predominates. The Hangendflötz also has the Stahlband as faux-mur. The roof and floor of all the seams are shaly sandstone with remains of plants. In the lower coal group, ferns predominate, in the upper group, cycads are abundant. These groups are separated by 97 meters of barren measures and Hantken is inclined to regard the upper one as belonging to the Middle Lias. About 74 meters of bituminous shale overlies the sandstone mass and contains streaks of coal as well as layers of iron ore. Some portions of this shale yield 3 to 7 per cent. of crude oil, from which paraffin and illuminating oil are obtained. The Liassic in this district is apparently of freshwater origin; the variations in thickness of the coal seams are due in very small part to compression, as is evident from the many illustrations given by the author.

Grand'Eury, in the memoir already cited, states that the coals at Anina and Bregheda rest on soils of vegetation. At Bregheda, where the coal is anthracitic, the mur and partings have many roots in place, some of them spreading out under the coal and much divided, while others are erect and cross several layers of the shale. At Anina, where the coal is fat, woody roots are in the mur and herbaceous roots in the partings.

The greatest thickness of coal is in the small area near Fünf-kirchen, where the coal group, consisting of alternating sandstones, marly shales, clay shale, coal seams and layers of iron ore, rests on Rhaetic beds and underlies the marine Middle Lias. It is about 800 meters thick. Not less than 180 coal horizons have been recognized,

with 25 to 28 workable seams. The thicknesses vary greatly and, at times, the rapid increase of earthy matter renders an important seam worthless. Mining operations are extensive and the horizons have been correlated closely. The succession of the thicker seams from below upward is

- I. and II., 24 to 36 inches, mostly unworkable;
- III., IV., VI., 36 to 48 inches, one half to three fourths good coal;
- VII., VIII., IX., 24 to 30 inches, occasionally too thin for working;
- X., 18 to 24 inches, a hard coal;
- XIII. to XIX., 12 to 24 inches, light, caking coal;
- XX., 20 to 60 inches, coal similar to the last;
- XXII., 0 to 60 inches, often absent;
- XXIV. to XXVIII., 20 to 24 inches, coal is hard.

Almost the whole of the formation was crossed in the tunnel at Vasas, where 174 seams were crossed in 717 meters. The total thickness of coal is 52 meters, but one half of it is unavailable because the seams are too thin or the coal is impure. 39 seams, with thickness of somewhat more than 14 meters, are marked as containing dirty coal.

The mining districts are Fünfkirchen, Szabolcs and Vasas. In the Fünfkirchen district, dips are 30 to 50 degrees and seams less than one foot are rarely mined; those of more than 2 feet are usually divided by partings. The mass, numbered XI. and XII. in the Vasas tunnel, consists of (1) clean coal, 0.40; (2) shale, 0.25; (3) clean coal, 0.40; (4) carbonaceous shale, 0.45; (5) clean coal, 0.48; (6) carbonaceous shale, 0.05; (7) clean coal, 0.25; (8) carbonaceous shale, 0.20; (9) clean coal, 1.00; (10) dirty coal, 0.60; (11) clean coal, 0.60; (12) shale, 0.05; (13) clean coal, 0.40; (14) carbonaceous shale, 0.20, resting on sandstone. The roof is shale containing mullusks. Other seams are double or triple and the partings are clay or carbonaceous shale. Of the 512 beds of rock cut by the Vasas tunnel, 8 contain marine fossils; three of them being in the highest portion, 70 meters, a transition to the overlying *Gryphæa* beds. Many marine mollusks have been obtained from the roof of coal III., the floor of XVIII. and the partings of XIII. and XXII. These are *Ostrea*, *Gervillia*, *Panopæa*, *Lima* and other off-shore

genera. Faux-mur and faux-toit are common. The dip is high and the coal is tender; of that mined at Fünfkirchen, only one per cent. is lump, pieces as large as a man's head; 20 per cent. is coarse, 20 millimeters or larger, while the remaining 70 per cent. is "dust"; volatile in this district is about 18, but in the Szabolcs district it is about 23. The coal is black, tender and in great part caking. The gas is low in illuminants.

The flora of Fünfkirchen consists of ferns, cycads and lycopods, some of which seem to persist throughout the Lower Lias. Leaf-bearing beds seldom overlie coal seams.

In the western part of the southern area, that of Neustadt-Törzburg, the coal-bearing Lias rests on crystalline schists and consists of brown, argillaceous, micaceous sandstone, which, through increasing content of plant remains, becomes darker and finally passes into carbonaceous shale, containing streaks of coal. The roof is a quartzose sandstone without trace of plants. In the eastern division, the schists are not reached and the coal group, consisting of sandstones, marls and coal seams, rests conformably on limestones. There seems to be but one coal seam, one to 2 meters thick, but the region is so broken by folding and faulting that a detailed section cannot be obtained.

Hantken called attention in the first edition of his work to the presence of roots in the floor of coal in the Steierdorf region; Zincken,²⁰ soon afterward, noted that near Kola, in the Steierdorf district the same horizon yields abundance of roots in vertical position. Gothan,²¹ having seen the root-bearing underclays associated with Jurassic coal seams on the Yorkshire coast of England, thought wholly probable that similar clays might be present in the Fünfkirchen area. His examination was successful though, owing to physical conditions, it covered only a portion of the district. At one locality, he found under coal VII. a characteristic underclay with irregular branching coaly markings, varying in direction and

²⁰ C. F. Zincken, "Ergänzungen zu die Physiographie der Braunkohle," Leipzig, 1878, p. 159.

²¹ W. Gothan, "Untersuchungen über die Entstehung der Lias-Steinkohlenflöze bei Fünfkirchen (Pecs), Ungarn," *Sitz. k. preuss. Akad.*, VIII, 1910, pp. 129-143.

wholly resembling roots. At another, he discovered a rhizome with its rootlets, which made the relations of the other markings clear. "Through such horizontal rhizomes, the analogy of the Mesozoic underclay with the Carboniferous *Stigmara*-beds and the recent or sub-recent reed beds is the more marked." Roots are rarely recognizable in freshly exposed rock but they are sufficiently distinct after slight weathering. Gothan removed the débris for some meters at several horizons and in one day he found well-marked underclays with roots, associated with 8 coal seams. In all, he uncovered such clays under 12 seams.

Spitzbergen.—Nathorst²² has described a sandstone group midway in his Jurassic of Spitzbergen. It contains coal seams and freshwater mollusks. A coal seam is exposed on the south side of Cape Bohemian, underlying sandstone and resting on shale or shaly sandstone. Leaves abound above the coal, *Ginkgo*, *Baiera*, with cycads and some ferns, and *Elatides* is under the coal. Bituminous sandstone with plant impressions and a seam of coal was seen at another locality, where, somewhat higher in the section, there is a soft clean sandstone with the same plants as well as freshwater mollusks, *Lioplax* and *Unio*; but still higher is a deposit with fossil wood and marine mollusks. The same group was seen on the shore of Van Keulen Bay, where the lower portion contains some thin coal seams and some clay ironstone.

Siberia.—Coal seams of Mesozoic age are present in extensive areas within Siberia. Their place in the column had not been determined when the description cited was prepared.²³ They were taken to be Jurassic, but they may be in part Rhaetic.

In the region between the Yenisei and Irkutsk rivers, the coal-bearing portion of the Jura, 60 to 90 meters thick, consists essentially of sandstone with subordinate beds of conglomerate and shaly clay. Fat and dry coals are here and boghead is not rare. A small area, about 10 kilometers square, of the freshwater Jura, near

²² A. G. Nathorst, "Beiträge zur Geologie der Bären-Insel, Spitzbergens, und des König-Karl-Landes," *Bull. Geol. Inst. Upsala*, Vol. X., 1910, pp. 362, 363, 365-369.

²³ "Aperçu des explorations géologiques et minières le long du Transsibérien," publié par le Comité Géologique de Russie, 1900, pp. 68, 86-92, 97, 179, 182, 190, 197, 199.

Tcheremkhovo in the government of Irkutsk, shows about 65 meters of friable sandstone, in which are 3 coal seams from a half meter to nearly 3 meters thick. The coal is good, caking and has from 3 to 10 per cent. of ash, though occasionally it has more, in one case, 25 per cent. The sulphur is low.

The Transsiberian railroad crosses the brown coal basin of the Middle Tchoulym River between the cities of Mariinsk and Artinsk. In this basin, embracing not less than 7,000 square kilometers, the rocks, almost horizontal, are sands, argillaceous sands, gravels, sandy or plastic clays, freshwater limestones and coal. The mass is 260 meters thick and contains numerous lenticular seams of brown coal. These have small areal extent, the largest being 2 or 3 kilometers long by a kilometer wide, but the maximum thickness in the lenses is from 2 to 6 meters, though in some instances it is far greater, 14 meters at one locality. The coal ordinarily rests on clay, with an intervening faux-mur, and passes upward into a friable coaly material, resembling peat, on which rests clay or sand. This brown coal is excellent, that from the mined portions of the lenses having barely 3 per cent. of ash, and the quantity in this field is said to be "colossal." Another area of brown coal was seen on the Upper Tchoulym River, but the quality is inferior, there being at times as much as 30 per cent. of ash. In other areas, farther west, some seams of brown coal are very thick. In the extensive region along the Angora River, the coals approach boghead in their general features and they have from 10 to 34 per cent. of ash; but some of the seams yield excellent caking coal.

No Mesozoic coal is reported from the Transbaikal region, where Jurassic deposits seem to be wanting; farther east, in the Upper Amur Basin, some coal seams were observed, which are thin and of no economic importance; but on the divide between the Amur and the Zéia Rivers, Jurassic beds occupy a vast area and consist of gray or greenish sandstones with conglomerates and coal seams. Excellent coal has been obtained from a seam on the Grande-Bira River. In the eastern provinces, rocks were found similar to those of central Siberia, with several seams of coal, one to 2 meters thick and yielding anthracitic as well as caking coals.

New Zealand.—According to Hutton,²⁴ conditions favoring accumulation of coal existed in New Zealand at several horizons, but only during brief periods. The seams are nowhere thick enough to repay mining. One, 6 feet, is merely carbonaceous shale with numerous streaks of coal.

Alaska.—The Jurassic area of northeastern Alaska was examined by Collier,²⁵ who made a reconnaissance survey of the Corwin formation, probably Upper Jurassic, between meridians 163 and 165, beyond the 69th parallel. The formation is present at 100 miles farther east and notes by other explorers lead to the belief that it extends far inland; Collier's studies were confined to the Arctic coast line. Lithologically, the formation consists of thinly bedded shales, conglomerates, sandstones and coal seams. Shales predominate, more or less calcareous, gray brown to black and vary from mere mudstone to sandy shale. The sandstones and conglomerates are few and seldom exceed 10 or 12 feet. The pebbles are of quartz and chert, the largest being about 4 inches in diameter. The thickness is at least 15,000 feet and the coal area within the district covers not less than 300 square miles. Mining operations were insignificant and the studies were made almost wholly upon outcrops.

The coal seams appear to be in two groups, Corwin, above, and Thetis, below, separated by a great thickness of barren measures.

The highest seam in the Corwin, 4 feet, 6 inches and without parting, is enclosed in black shale or shaly sandstone. Some thin beds and impure coals were seen in the interval, 1,000 feet, to the next workable seam, which is 5 feet thick and divided by two thin partings of clay. Its roof is shaly sandstone and the floor is hard clay. The next seam, 500 feet lower, is the Corwin, which was opened many years ago, but the opening was inaccessible at the time of Collier's visit, being covered by a great snowdrift. This seam, about 1,000 feet above the bold conglomerate of Corwin Bluff, is said to be 16 feet thick, of which 7 feet are practically clean coal,

²⁴ F. W. Hutton, "Geology of Otago," Dunedin, 1875, pp. 99, 100; Geol. Survey of New Zealand, Reps. for 1873-74, p. 36.

²⁵ A. J. Collier, "Geology and Resources of the Cape Lisburne Region, Alaska," U. S. Geol. Survey, Bull. 278, 1906, pp. 27, 28, 37-40.

the rest being so badly broken by partings as to be worthless. The interval to the conglomerate of Corwin Bluff is filled with shale, holding at least 8 coal seams. The cliff could not be reached and the thicknesses of only three could be estimated: 4, 12 and 30 feet. An irregular seam underlies the conglomerate and rests on sandstone; it is in pockets but the coal is good in spite of the distortion. Lower seams were seen in the next 1,000 feet, not distorted, as they are in soft shale, which took up the strains.

Below the lowest seam of the Corwin is a series of barren measures, about 8,000 feet, in which only thin streaks of coal were seen; this overlies the Thetis group, which is reached at 6 miles east from Corwin Bluff and its highest seam is known as the Thetis, 6 feet thick, and opened many years ago. Ten seams were found in the succeeding 700 feet of shale, only two of which are likely to prove important.

This necessarily imperfect record suffices to show that the quantity of Jurassic coal in northwestern Alaska is enormous. Some cannell is said to have been found in the Corwin group, but Collier saw none.

JURA-TRIASSIC.

Generally speaking, it may be said that where the succession is complete, there is always a portion of the column, which is debatable ground, and there is difficulty in determining the boundary between formations. In some cases, unconformities due to folding or to erosion offer evidence on which to base a final determination; but such areas, though large in square miles, often mark only local adjustments, similar to those observed within formations, but which no one regards as important. Occasionally, the matter is complicated by lack of fossil remains. Such is the condition in a great part of Australia, where it has not been possible to divide satisfactorily the great mass between the Permo-Carboniferous and the Cretaceous. Jack and Etheridge²⁶ recognize a Trias-Jura system in Queensland, which Jack has divided into the Ipswich and Burrum formations.

²⁶ R. L. Jack and R. Etheridge, Jr., "Geology, etc., of Queensland," 1892, pp. 300-39, 366.

The Ipswich or newer formation occupies an area of about 12,000 square miles in southeastern Queensland and consists, for the most part, of fine conglomerates, grits, sandstones and shales with seams of coal and beds of fireclay. At a few miles south from Brisbane, W. H. Rands saw a mass of coal and carbonaceous shale, 12 to 13 feet thick. The "best" coal is in the lower portion; some pieces of hard bright coal, free from shale partings, contained 24 per cent. of ash. A seam in the same neighborhood shows (1) coal, 4 inches; (2) shale, 2 feet, 2 inches; (3) coal with bands of shale, 1 foot, 6 inches; (4) good, hard coal, 5 feet, 3 inches; (5) shale, 3 inches; (6) fireclay, 2 inches; (7) shale with bands of coal, 5 feet, 6 inches; (8) fireclay, 1 foot, 4 inches; (9) coal, 2 feet; (10) black band, 8 inches; (11) coal, 5 feet, 3 inches; (12) hard sandstone, 2 inches; (13) coal, 4 inches; in all, 24 feet, 11 inches with somewhat more than 14 feet of coal aside from the thin bands of coal in the thick shale division. A piece from No. 11 had 19 per cent. of ash. A shaft in this district cut one foot of cannel and, lower down, a seam of hard and bright bituminous coal, but the sample from it contained 31.61 per cent. of ash. The coals in this district are much broken by partings and high in ash; yet, there were times and places during and in which conditions favoring accumulation of clean coal existed; for a piece taken from a thin bench at one locality showed only 2.5 per cent. of ash.

The type district, that of Ipswich, about 30 miles west from Brisbane, was examined by A. C. Gregory. The best seam near Ipswich is 5 feet, 6 inches thick and contains 3 to 4 feet of coal, of which the best contains about 11 per cent. of ash. Beyond Brisbane River, the seams contain comparatively little coal and that is usually poor; but one of them becomes 4 feet, 6 inches at one locality and its coal has barely 9 per cent. of ash. This seam, however, deteriorates in all directions. This variability characterizes seams throughout the district; a thin seam may be disseminated in a mass of coaly shale, 20 to 30 feet thick. Gregory ascertained that the quality of coal bears some relation to its distance from the northern margin of the field, the ash increasing in that direction—that is, toward the border of the great valley in which the coal measures accumulated.

Going westward from Ipswich along the railway to Toowoomba, one reaches lower members of the formation, which have seams of cannel at many localities; the associated rocks are sandstone and shale. A thick seam on Blackfellow's Creek shows (1) coal, 1 foot; (2) fireclay, 1 foot; (3) coal, 6 feet; (4) white clay, 1 foot; (5) coal, 1 foot; (6) clay shale, 1 foot; (7) coal, 1 foot; (8) a thick bed of fireclay and shale. The coal in all benches is hard cannel, so that the whole of it is available. There are some seams of bituminous coal, caking, in this region but they are thin. Near Clifton station on this railway, a shaft cut three seams at 60, 80 and 100 feet from the surface. The lowest is a rich, very hard "oil coal"; the middle seam yields good caking coal and the highest, 4 to 5 feet thick, consists of bright bituminous to dead-black "oil coal," all being hard and tough. From the description, it would appear that the cannel is in lenses within the bituminous coal. The town of Warwick is on an outcrop of sandstone, which holds a great quantity of fossil wood, usually replaced with iron ore. The coal between Warwick and Walloon is mostly cannel, which yields a high percentage of gas or of oil and paraffin.

The only mollusk recognized is *Unio*. *Vertebraria* is in the underclay of a coal seam near Tivoli. From various horizons, there were collected 11 genera of ferns, 4 of cycads and 5 of conifers.

The Burrum formation or lower portion of the Trias-Jura is exposed in a continuous area of about 3,000 square miles as well as in some small areas. Not much development had been attempted prior to 1892, owing to lack of railroad communication; but comparatively extensive operations were under way near Howard, about 150 miles north from Brisbane. There W. H. Rands measured a section of 1,015 feet, representing the top fifth of the formation and containing 6 seams, 1 foot, 8 inches to 5 feet thick, which were mined. These coals are of good quality, low in ash, are caking and yield a good gas for illuminating. The coal seams generally are irregular. The fauna is scanty, a few specimens of *Corbicula* and of *Rocellaria* have been seen. The flora is almost equally scanty and is represented by a few fragmentary specimens belonging to 4 genera of ferns, 2 of cycads and one conifer.

In New South Wales,²⁷ strata seen on the Clarence River District have some insignificant streaks of coal and the flora has Jurassic affinities. The rocks are conglomerates, sandstones and shales, and the coal seams are unimportant. The Wianamatta beds, about 700 feet thick, are older and more argillaceous. Entomostraca occur in the upper layers. The coal seams are, at most, only a few inches thick. The Hawkesbury series, resting on the Permian-Carboniferous, is about 1,000 feet thick and consists of yellowish-white sandstone with a few beds of shale and conglomerate and some streaks of coal, without economical importance. The sandstones show much false bedding, usually directed toward the northeast, but reversal of the currents is evidenced by occasional inclination in the opposite direction. Contemporaneous erosion of the sandstones is proved by old channel-ways filled with gravel and angular boulders are not rare. Wilkinson thought the false bedding due to currents in shallow water; but he cites J. E. Tennison-Woods, who asserts that the peculiar structure is evidence that these sandstones are a wind-blown formation. Plant leaves and fragmentary stems as well as remains of fishes are in both formations but no remains of marine animals had been discovered. The later studies of the New South Wales geologists make it clear that the relations of the Wianamatta and Hawkesbury to the Triassic are very close.

TRIASSIC.

The term Trias is of German origin; on much of the continent, the system is triple or was recognized as triple, being divided into the Keuper, Muschelkalk and Bunter. In later years, the Rhætic or Infra-lias has been taken to be more closely allied to the Trias, so that now the divisions are four.

Within Great Britain, Rhætic, Keuper and Bunter have been recognized, but the Muschelkalk or limestone division seems to be wanting. The several formations consist of conglomerates, shales, marls and sandstones; the Bunter in considerable areas passes downward gradually into the Permian. Rock salt and gypsum are in the

²⁷ C. S. Wilkinson, "Notes on the Geology of New South Wales," Dept. of Mines, Sydney, 1882, pp. 53-55.

Upper Keuper. The whole mass is apparently without coal. The sandstones in very many cases are false bedded, suggesting wind-drift structures; footprints abound at numerous localities. The general features have led some English geologists to believe that the Trias of that country was formed during desert conditions. On the continent, coal was formed during the Upper Keuper as well as in the Lower or Kohlenkeuper. There appears to be none in the Muschelkalk or Bunter sandstone. Salt and gypsum are in the marls of Upper Bunter, footprints are numerous in the Middle, while the sandstones of the Lower Bunter are usually false bedded and footprints are abundant. As in England, the Bunter of north and central Germany passes gradually downward into the Permian.

Sweden.—Coal is present in the Rhætic of Sweden. Hebert²⁸ states that at Ramloesa, 4 or 5 kilometers southeast from Helsingborg, he measured a section of somewhat more than 240 feet, consisting mostly of black shale, with a streak of coal, 2 centimeters, at the top, and another, 3 decimeters, at the base. The latter was mined. The shales associated with this coal yielded no plant remains to Hebert, but other collectors had obtained specimens, which are in the museum at Lund. Plant impressions were seen in a sandstone, midway in the section. Plant structure is distinct in the coal. Geikie,²⁹ summarizing results obtained in this region by Nathorst, E. Erdmann and G. Lindstrom, says that the area of these Rhætic beds is about 250 square miles. They have been divided into a lower, freshwater group, containing workable coal seams, and an upper, marine group with only poor coal but abundant marine organisms. Clay ironstone occurs in the lower group and beds of fireclay underlie the coal seams.

France.—Servier³⁰ described the Keuper area of the Vosges, northeastern France. The Upper Keuper is triple; variegated marls on top, dolomitic limestone in the middle; the lower division is (1) variegated marl, 1.50; (2) micaceous sandstone, more or less

²⁸ E. Hebert, "Notes sur les grès infraliasiques de Scanie (Suede)," *Bull. Soc. Geol. France*, II., Vol. 27, 1870, pp. 366-376.

²⁹ A. Geikie, "Text-Book of Geology," 3d ed., 1893, pp. 870, 871.

³⁰ M. Servier, "Notes géologiques sur les mines de houille de Norroy (Vosges)," *Bull. Soc. Ind. Min.*, t. IV., 1858-59, pp. 384-398.

argillaceous, with abundant impressions of plants and animals, 3.30; (3) laminated shale, argillaceous, with leaf impressions, 0.05 to 0.15; (4) coal, 0.25 to 1.00; (5) black-brown carbonaceous shale, with great abundance of vegetable impressions, ill-preserved but remarkably like modern swamp plants, such as reeds and ferns, 0.50; (6) marly shales with plant impressions and *Posidonia*, 0.90; (7) shaly sandstone with remains of plants, 0.50; (8) silicious fetid limestone, 3.00; total, 10.40 meters. This rests on the Lower Keuper, mostly variegated marls with gypsum and salt. The dolomite marks a notable change in conditions; below it, the deposits are micaceous and sandy, with abundant remains of plants and animals; but above it, marls predominate and remains of any sort are rare.

The coal seam varies greatly in thickness; at times it bifurcates, at others it disappears. These variations are not due to disturbance as the dip is less than 3 degrees. Kidneys of dark calcareous iron ore are in the coal, now concentrated under the roof but again scattered throughout the seam. Pyrite is abundant. Where thickest, the seam is triple, showing (1) upper bench, variable, consisting at times of alternating bright and dull laminations, when the coal is rejected as it burns badly and is not reduced to ash; commonly, however, it is brilliant black and an excellent fuel; (2) middle bench, not always present; its coal is glossy black, is almost uniform, burns well and is reduced to red ash; it encloses vegetable remains, some of them root-like; (3) lower bench, has brilliant black coal, yielding a brown powder.

The quality and thickness improve toward the north. At the south, near La Marche, Romain and Talliancourt, it is replaced with clays containing great numbers of tree stems. Mining begins farther north near la Rouville and Croinville, where the thickness is 0.15 to 0.30; at Norroy, it becomes 0.40 to 0.80, but at Gemmalaincourt and Parey it is 1 meter. Fragments of shale, quartz and sandstone with rounded angles occur occasionally in the coal. The lenticular form of the seam is distinct.

The same horizon has been recognized at widely separated localities in France, though coal is rarely present. Rouville,³¹ describing

³¹ P. de Rouville, *Comptes Rendus*, t. 48, 1857, pp. 696-698.

the Trias of Aveyron and Herault, states that the abundant coaly impressions of plants in Keuper beds had induced many to search for coal but without success. Grand'Eury saw some coal in the Keuper of Nice which contains stems of *Equisetites* and in the shale are rootlets of these plants. At Gemmalaincourt, he found *Equisetites* roots in the underclay but bark and seeds are in the coal.

Germany.—The Lower or Kohlenkeuper contains at many places in Germany the Lettenkohle, which Credner³² describes as a carbonaceous clay, filled with plant remains and at times passing into impure coal. Near Siwierz in Poland there are 3 beds 30, 50 and 80 inches thick. Sandberger³³ published records of numerous sections of Triassic deposits obtained in Unterfranken of Bavaria. He offers no comments, but the records suffice to prove irregularity of deposit. Two Lettenkohle sections near Würzburg exhibit the triple structure. That obtained between Würzburg and Rothen-dorf shows at top of the middle division a yellow fine-grained sandstone with many erect roots, while at base of the division is a zone with abundant remains of plants. This rests on the Hauptsandstein of the lower division, part of which is diagonally bedded. No coal is present. In the other section, between Würzburg and Schweinfurt, plant remains abound in both the upper and the middle division, but coal is wanting; the top layer of the Hauptsandstein is argillaceous sandstone with many roots, while at the base is a fine-grained sandstone with irregular layers of pulverulent coal. A section of the Krainberg gives these details respecting the middle division: (1) clay shale, with Lettenkohle at base, 3.66; (2) shale, 0.15; (3) sandstone with roots, 1.18; (4) clay shale, 1.18; (5) Lettenkohle and plants, 0.70; (6) ochreous limestone, 1.32; below which to the base are sandstone, ochreous limestone, clay shale and sandy shale, all apparently without coal. The sandstone, No. 3, is the root bed for plants which produced the impure coal above it.

The conditions seem to have been much the same at all localities where Lettenkohle exists. The coal is irregular in occurrence and

³² H. Credner, "Elemente der Geologie," 8te Aufl., 1897, p. 535.

³³ F. v. Sandberger, "Die Lagerung des Muschelkalk- und Lettenkohlen Gruppe in Unterfranken," *Verh. Phys. Med. Gesells. Würzburg*, Band XXVI, 1893, pp. 200, 205, 206.

usually is of little value. The influx of foreign matter into the petty swamps was too great to permit accumulation of clean coal; but root-bearing underclays and soils of vegetation without coal are characteristic features. v. Gümbel⁸⁴ states that Lettenkohle from Guildorf in Würtemberg and Schweinfurt in Franken gives a weak brown tint to solution of caustic potash; it is easily decomposed by Schultze's solution and woody structure is distinct in the residue. Rhætic coal from near Bayreuth reacts to Schultze's solution as does Lettenkohle. Many layers of this coal appear to consist almost wholly of pollen exines.

Austria.—An important area of Triassic coals is in Upper and Lower Austria; these belong to the Lunzer beds of the Upper Keuper. A less important area is in Südtirol, where coal is in the Wengener beds at the base of the Keuper.

The Upper Keuper area was studied by Lipold⁸⁵ and his associates. The Triassic deposits are in the interior of the northeastern Alps and they have suffered more from disturbance than have the Liassic beds of that region. Lipold reports that near Baden, on the eastern side of the area, the coal and shale are so crushed and intermingled that definite sections cannot be made and that all attempts to obtain merchantable coal have failed. No mollusks were seen but *Calamites arenaceus* and *Pterophyllum longifolium* are not rare.

Hertle found only unimportant seams in the Lunzer sandstones near Ramsau; but in Kleinzell, where the sandstone is much distorted, 3 thin seams were seen, all marked by extreme variations in thickness, which seem to be due to compression during folding. At Lilienfeld on the Traissen River, the dip is from 40 to 70 degrees and the coal seams, being between sandstones, have been distorted seriously. The thickness of one seam varies from one inch to 9 feet within a short distance. The Lunzer sandstone is distinctly of freshwater origin in this district, but it is between the Opponitzer above and the Goslinger below, both of them calcareous and containing marine fossils. The workable coal seams, 4 and 2 feet thick,

⁸⁴ C. W. v. Gümbel, "Beiträge, etc.," p. 160.

⁸⁵ M. V. Lipold, G. v. Sternbach, J. Rachoy, and L. Hertle, "Das Kohlengebiet in den Nordöstlichen Alpen," *Jahr. k. k. Geol. Reichs.*, Band 15, 1865, pp. 62-159.

are in a mass of black shale, about 70 feet thick. *Equisetum columnare* is abundant in the black shales and beautiful specimens have been obtained from the roof of the upper seam. This seam, 4 feet thick where first seen, is from 3 to 24 feet. Occasionally it divides into two or more benches, of which only one is persistent. The coal of Lilienfeld and Kleinzell yields 72 to 74 per cent. of good coke and ash is from 8 to 14 per cent. in the raw coal.

Hertle examined the area near Kirchberg on the Pielach River where the black shale mass has 4 seams of coal. This shale is 40 feet in one tunnel, 48 to 60 in another, while in a third it is not less than 100 feet. In one tunnel, the middle seam is 72 feet above the lower one; followed westward, the interval becomes 50, 30 and 18 feet. A similar convergence is that of the middle and upper seams, which actually unite with increased thickness. These relations existed before disturbance occurred. Dips in this district are from 40 to 70 degrees. The coal throughout is tender and caking, giving 67 per cent. of good coke; but the ash is high, averaging 15.8 per cent. In the Rehgarten area, the coal is cleaner, having only 9 per cent. of ash. Here distortions of the rocks are few but other troubles are encountered; the seams thin away and frequently they pass into carbonaceous shale. Hertle's descriptions make it clear that the seams are lenses, sometimes joined by carbonaceous shale, but at other times wholly separate. The "horseback" seems to be a feature here, as in the older as well as in the newer coals. One tunnel reached sandstone, with no admixture of clay or coal, at 480 feet from the mouth. It was pushed through the rock and again reached the coal. The lower seam at Loichgraben yields a good coal, but that from the upper seam has 52 per cent. of ash, though it looks like excellent coal.

Rachoy found plant-bearing shales as roof of coal seams near Lunz and he says that, near St. Anton, a bituminous limestone is the roof in some mines. The coal at several localities is good but at others the ash is very high, while the coal externally resembles the best in the district. This area is on the westerly side of the Lunzer region and, in most cases, the seams are thin.

Zincken³⁶ states that plant-bearing shales are the roof at many

³⁶ C. F. Zincken, "Ergänzungen, etc.," 1878, pp. 110, 111.

localities; that the coal seams are distinctly lenticular in some of the important districts, and that the coal is caking at some places, but non-caking at others.

The Wengener beds are at base of the Keuper and rest on the Muschelkalk. Keyserling⁴⁷ found coal within these beds, west from Cordeville Valley on the southeasterly slope of Mt. Cordai in south Tyrol. The rocks are alternating tuff sandstones, red, green and brown clays and marls, interrupted by beds of limestone. All yield so readily to the weather that a detailed section cannot be made. The Hauptflötz, locally regarded as "workable," is from 4 to 5 decimeters thick and is well exposed in the bed of a stream, where it rests on dark limestone; elsewhere, it is frequently enclosed in clay and sandstone. The coal is laminated, some of it resembling brown coal but other portions are much like stone coal. The transformation is so far advanced that no trace of organic structure can be recognized by the naked eye, but the mode of occurrence convinced the author that it was derived from water-loving plants. The quantity of pyrite is remarkable. Coal rarely occurs at this horizon.

The Lunzer horizon was recognized by Lipold³⁸ in Carniola (Krain) who saw near Idria coaly shale with streaks of coal, but he could discover no definite seams.

Hungary.—Hantken³⁹ reports that in the Fünfkirchen region of Hungary a sandstone formation, 620 to 950 meters thick, underlies the Liassic coal complex conformably. Its coals appear to be local and in most cases they are too thin to be mined. Fossils are not abundant; at one locality, *Zamites*, *Palissya* and *Thaumatopteris* have been collected; another yielded *Cardinia* and *Acrodus*. This assemblage is accepted as evidence that the mass is of Rhætic age.

United States.—Triassic deposits of the Atlantic border extend in detached areas from Massachusetts to North Carolina. No coal of economic importance has been discovered north from Virginia, though thin streaks have been observed in Massachusetts, Rhode

³⁷ H. G. Keyserling, "Ueber ein Kohlenvorkommen in den Wengener Schichten der Südtiroler Trias," *Verh. k. k. Geol. Reichs.*, Jahrg. 1902, pp. 57-61.

³⁸ M. V. Lipold, *Jahrb. k. k. Geol. Reichs.*, Band 24, 1874, p. 445.

³⁹ M. Hantken, "Die Kohlenflötzen, etc.," pp. 104, 105.

Island and Pennsylvania. McCreath⁴⁰ states that P. Frazer had found coal in Triassic beds of York County, Pennsylvania, but neither he nor Frazer in his York County report gives a description of the deposit. According to McCreath, the coal is deep black, with pitchy luster, brittle and with conchoidal fracture. The proximate composition is: Water at 225° F., 4.310; volatile, 18.482; fixed carbon, 74.358; sulphur, 0.528; ash, 2.322. There is no tendency to cake and the gases burn with non-luminous flames. The dried coal absorbs water with great avidity, so that within a few hours it re-absorbs about 63 per cent. of the water originally present.

The important region known as the Richmond coal field is reached at a little way north from the James River in Virginia. Mining operations were begun a century ago and for many years they were on extensive scale. Irregularities in the seams and the many faults made mining costly and the local coal was displaced by anthracite from Pennsylvania. Operations now are unimportant.

Fontaine,⁴¹ in the introduction to his descriptions of fossil plants obtained in the Richmond and adjacent areas, gave a synopsis of the relations. The Triassic rocks occupy several areas in a belt extending from Rhode Island to South Carolina. The most westerly area, termed the Palisade, is almost continuous from the Hudson River across New Jersey, Pennsylvania and Maryland to about 75 miles southwest from the Potomac River in Virginia; it is without coal. The small area of Buckingham County, Virginia, is east from the last and like it is without coal. The Dan River area, still farther east, is in Virginia and North Carolina; it has some coal in the latter state. The Cumberland (Farmville) area is small but has some coal seams of local importance. The Richmond, 30 miles east from the Cumberland, is the last in Virginia, but the Deep River, still farther east, is in North Carolina and extends to the South Carolina border.

Red beds prevail in the western areas but they are insignificant in the Cumberland and Richmond areas. Fontaine recognized three

⁴⁰ A. S. McCreath, Second Geol. Survey Penn., Report MM, 1879, p. 103.

⁴¹ W. M. Fontaine, "The Older Mesozoic Flora of Virginia," U. S. Geol. Survey, Mon. VI., 1883, pp. 1-7, 12-16, 32, 45, 79.

distinct groups in the Virginia areas: the upper group, consisting of loose granitic sandstone or sandy shale, containing no coal but much lignite, resembling jet; silicified wood is not rare; a middle group, coal-bearing, with a large proportion of black shale; a lower group, sandstone and shale. The sandstones of the lower group are not easily distinguished from the underlying granitoid gneiss and are 100 to 600 feet thick in the Richmond area. The middle group is 100 to 200 feet thick in the same field, where it usually has two thick seams of coal—but the number, thickness and quality vary greatly. At many places the roof is a plant-bearing shale; *Equisetum rogersi* is usually associated with *Macroteniopteris* and its casts are present in the coal. *Schizoneura* occurs in the underclay of the main seam. The plants described by Fontaine are conifers, cycads, equiseta and ferns.

Shaler and Woodworth⁴² applied names to Fontaine's groups; the Chesterfield or upper group is 2,500 feet thick and consists of sandstone above, shales below; the Tuckahoe, equivalent to the middle and lower groups, consists of the coal measures, 500 feet, more or less, sandstones and shales, 0 to 300 feet, and boulders, 0 to 50 feet.

The Richmond field was discussed many years ago by geologists, who studied it when the mines were still in operation.⁴³ It is well to summarize the statements of each observer as the conclusions reached by them have been regarded as not in agreement and they appear to be in some respects contrary to those reached by observers who have studied the region since mining operations practically ceased.

Taylor reported that the deposits occupy a narrow trough, which deepens so rapidly toward the median line that coal mines are pos-

⁴² N. S. Shaler and J. B. Woodworth, U. S. Geol. Survey, 19th Ann. Rep., Part II., 1899, p. 423.

⁴³ R. C. Taylor, "Memoir of a Section Passing through the Bituminous Coal-Field near Richmond, Virginia," *Trans. Geol. Soc. Penn.*, Part I., 1835, pp. 275-297; W. B. Rogers, "Reprint of Annual Reports on Geology of Virginia," 1884, pp. 62-69; "On the Age of the Coal Rocks of Eastern Virginia," *Reps. Amer. Asso. Geol. and Nat.*, 1843, pp. 298-316; C. Lyell, "A Second Visit to the United States of North America," 2d ed., London, 1850, pp. 281-287.

sible only on the eastern and western margins. The maximum thickness of coal, as far as can be ascertained, is near the middle of the eastern border, whence it thins toward the north and the south. The coal in all mines, of which Taylor gives measurements, is near the base of the section and rests on the granite or is separated from it by, at most, a few feet of shale. The overlying rocks, for about 400 feet, as cut in shafts on both sides of the trough, are mostly grits, sometimes conglomeratic, with interstratified gritty micaceous, carbonaceous or argillaceous shale.

In the northeastern part of the trough, he saw two seams, 5 and 3 to 4 feet, separated by 10 or 12 feet of slate and about 10 feet from the granite, there being a thin seam in the latter interval. On the northwestern side, the seams are 30 feet apart and are 6 to 16 and 4 to 8 feet thick. These are said to unite farther north. The lower seam, of rather inferior quality, rests on the granite. On the eastern border, the Chesterfield shaft shows (1) coal shale, 6 feet, 10 inches; (2) coal, 5 feet, 6 inches; (3) coal shale, 3 feet; (4) coal, 1 foot, 6 inches; (5) hard grits, 2 feet, 6 inches; (6) shale and thin coal, 2 feet, 6 inches; (7) coal, 7 to 40 feet; (8) granite. The lowest coal has some variable partings. The sections on this side of the trough are much alike; but the coals, 4 and 6, are not always present and not infrequently some shale was seen between the coal and the granite.

As the mines had been worked extensively prior to Taylor's visit, he had opportunity to examine considerable spaces from which the coal had been removed so that the underlying granite surface was exposed. Not rarely a boss of granite rose through the lower division of the seam; in such cases, the work was usually abandoned; but occasionally a drift was carried around the boss and entered a body of coal, filling a hollow, 50 or 40 feet deep. There is no parallelism between top and bottom of the seam. The roof is irregular, rising and falling, and the depressions sometimes reach the floor, but they never conform to the irregularities of the granite surface. In spite of these irregularities, the lamination of the coal is wholly undisturbed. The lower part of the seam is less clean than the upper, but the coal is fat and coking throughout.

Rogers was studying the region at the time of Taylor's visit.

His report, published in 1836, contained a brief statement which adds important observations while confirming those made by Taylor. He discovered that the overlying sandstone group apparently overlaps the coal measures and that the lowest coal seam is separated from the granite in most cases by only a few feet of shale. The coal thickens toward the center of the basin and, as a rule, the higher seams are the best.

In the Midlothian and several adjacent mines, there is ample evidence to prove that the coal accumulated in saucer-shaped basins to the thickness of 40 or 50 feet, while on the eminences of the same floor it is thin. On the south side of the James River, the River pit was abandoned when the granite floor rose almost to the sandstone roof. Near Tuckahoe, on the north side of the river, the coal was found central in a small, isolated, cup-like depression. This coal rose gently in all directions from the shaft and thinned from 5 to 2 feet toward the edges of the shallow basin. This is several hundred feet in diameter and its strata vary little from the original nearly horizontal position. "Everything lends countenance to the opinion that the surface of the primary rock, previous to the deposition of carbonaceous matter, was a valley of rolling outlines, occupied by hollows and elevations, causing the first layers of matter, which were thrown down, to be deposited in greater thickness in some places than in others. As the lowest coal seam is separated from the crystalline rock by only a very few feet of shale and in some cases by none at all, it appears likely that the distribution of the coal was made unequal in thickness from the very commencement."

In his later memoir, discussing the relation of the plant remains, Rogers stated that the most abundant plants are *Equisetum columnare*, *Taniopteris*, and a large species of *Zamites*. These occur in vast numbers immediately upon the coal or interlaminated with it. They are accompanied by *Calamites*, *Pecopteris* and *Lycopodites*. The *Equisetum* is so abundant, at times, as to give a coarse coal consisting of alternate laminations of coal and shale with occasionally 30 laminations to the inch. Ferns are rare, aside from the great *Taniopteris*. The only animal remains are those of fish and some teeth supposed to be reptilian. The fish remains are in dark

shale associated with the coal; but scales along with teeth and plant impressions were seen at times in the upper part of the coal itself. Rogers saw nothing answering to the *Stigmara*-clay of the Carboniferous. These descriptions by Rogers make clear that a faux-toit is the ordinary feature; while the presence of animal remains in the coal indicates existence of pools on the swamp surface. Underclays are in this field, but they do not hold *Stigmara*, for *Lepidodendron* and *Sigillaria* had become extinct.

Lyell visited this field in 1845. He was much impressed by the fact, already noted by Rogers, that stems are found so often erect and compressed vertically; he could think of no reason to doubt that the greater number of such plants, in beds above and between coal seams, and which he saw at localities miles apart, had grown where they are now enclosed in sand or mud. The great coal seam rests at times directly on the granite, but at others is separated from it by an inch or two of shale. He was inclined to think that the absence of deposits between the coal and the granite may be due to disturbances, which were considerable, as shown by the extensive faults.

Mining operations ceased at nearly all localities about 50 years ago and the old mines, abandoned, soon became inaccessible. A long interval passed before new studies were made and few⁴⁴ of these dealt with details respecting the coals. Fontaine's detailed stratigraphical work was done near Clover Hill in the southeastern part of the field, where some work was going on at the time of his examination. There he found thick deposits between the coal and granite and assigned to them a thickness of 100 to 600 feet. Clifford stated that in outlying districts of the Richmond basin there is only one coal seam, usually of great thickness and separated from the granite by a thin bed of shale, often not more than a few inches. This refers to the northern part of the field. It should be noted here that the earlier observers regarded the benches of coal as separate seams.

⁴⁴ W. M. Fontaine, "The Older Mesozoic Flora of Virginia," U. S. Geol. Survey, Mon. VI., 1883; W. Clifford, "Richmond Coal Field, Virginia," *Trans. Manch. Geol. Soc.*, Vol. XIX., 1888, p. 320; I. C. Russell, "The Newark System," U. S. G. S. Bull. 85, 1892, pp. 38-40, 63; N. S. Shaler and J. B. Woodworth, "Geology of the Richmond Basin, Virginia," 19th Ann. Rep. U. S. G. S., Part II., 1899, pp. 423-426, 429, 483.

Russell asserts that the coal seams of the Richmond basin are irregular and greatly disturbed by faulting. They are not continuous though they are approximately at the same horizon. He regards them as overlapping lenses, individual deposits thinning away. A thin seam in one mine may be the important one in another. As to the interval to the granite, he cites O. J. Heinrich, who in 1879 reported that at Midlothian the coal is at 570 feet from the granite; also Fontaine, who in 1883 stated that the interval at Clover Hill is 250 feet. Russell suggests that the luxuriant subtropical vegetation of these Triassic lowlands has its nearest modern analogue in the fern forests of New Zealand. The ground must have been covered with ferns, above which rose equisetæ and the great ferns with palm-like leaves; cycad forests with pines of Araucarian type covered the upland.

Shaler and Woodworth report that the lower barren beds, underlying the coal measures, are not always recognizable with certainty; sometimes the barrenness may be due to lack of coal accumulation at the locality, but there are places where the coal group is fully developed and where a considerable thickness of barren rocks was seen. These authors offer no explanation of the origin of the boulder beds occasionally observed at the base of the section. They consist of granitic boulders with a partial bedding of reddish gritty sandstone. Plate XXI. of the report illustrates well the disintegration of the granite, which preceded deposition of Trias in this basin. This is remarkably similar to conditions observed by the writer in central France between Aurillac and Decazeville, where such disintegration is shown at many places. In the Decazeville basin, this preceded the deposition of the Coal Measures and the accumulations were mistaken for deltas by several observers.

Some have supposed that the great variations in thickness of the Richmond seams were caused by pressure during disturbance; but there appears to be no reason for resort to this explanation. Such swelling and contraction of seams is certainly common enough in disturbed regions, but there the structure of the coal is changed; it is exceedingly tender or it is rolled into flakes like pastry. But in the Richmond basin the lamination, according to Taylor and according to observations by the writer, is undisturbed in locali-

ties where the coal is very thick. Several observers have urged that the varying interval between the coal and the granite floor is likewise a result of disturbance. This suggestion may, perhaps, prove good for some localities but to the writer it seems unnecessary to resort to that hypothesis; Rogers's suggestion is far better, that the deposits were made on an irregular surface. This accords with the conditions observed in North Carolina as well as in Virginia.

Two Triassic areas are in North Carolina; the Dan River, at the northwest, is without coal in Virginia but has some irregular deposits in North Carolina; the Deep River, at the southeast, begins near the Virginia line and extends as a narrow strip southwestwardly into South Carolina.⁴⁵

Emmons's section in the Deep River area shows a triple structure: Upper red sandstones and marls; Coal measures, slates, shales and drab sandstones; Lower red sandstone with conglomerate at base. The red rocks, wanting in the Cumberland and Richmond areas of Virginia, reappear here on the southeasterly border. The middle group, about 1,200 feet thick, has fine-grained sandstones which frequently are rippled; the coal seams are few and very irregular but some of them have been opened. Russell states that at Egypt a shaft reached, at 422 feet from the surface, a coal seam showing (1) black shale; (2) coal, 2 feet; (3) black band, 1 foot, 4 inches; (4) coal, 1 foot, 1 inch; (5) slate, 6 inches; (6) coal, 7 inches. Another seam, 25 feet lower, has black band roof and floor and is one foot thick; the upper seam has black shale roof and floor. Both are irregular in thickness and Russell asserts that there is no reason to suppose that they are continuous in any considerable area.

The coals are indefinite within the Dan River area. Emmons reports that, near Leakesville in northern part of the area, a coal seam shows: (1) coal, semibituminous, 2 to 3 feet; (2) micaceous shale, 2 feet; (3) coal, shaly, 1 foot, 6 inches. This is very near the base of the coal group. The lowest rock at the southern extrem-

⁴⁵ E. Emmons, "Geological Report of the Midland Counties of North Carolina," 1856, pp. 228, 230, 235, 256, 257; I. C. Russell, Bull. 85, p. 41; W. C. Kerr, "Report of the Geological Survey of North Carolina," Vol. I., 1875, p. 143; R. W. Stone, "Coal on Dan River, North Carolina," Bull. 471-B, 1812, pp. 5, 6, 16.

ity, near Germanton, is a conglomerate of angular fragments of granite and gneiss, containing roots of silicified tree-stems penetrating and branching in the deposit. The stems are very abundant just above the conglomerate, so abundant as to suggest that they are remains of an ancient forest. Most of them are prostrate and occasionally one finds the roots converted into lignite. The great abundance of stems near Germanton in Stokes county impressed Kerr, who says "the public road being in a measure obstructed by the multitude of fragments and entire trunks and projecting stumps of a petrified Triassic forest; and similar petrifications are abundant in the Deep River belt, occurring in this as in the other among the sandstones near horizons of the coal."

Stone's examinations led him to assign a thickness of about 7,800 feet to the deposits within the Dan River area, where the mass rests on Archean gneiss. The zone of carbonaceous shale with coal is 250 feet thick and just below it, at about 1,000 feet from the base, is conglomerate with subangular fragments, which is absent from the northern portion of the area. The roots and bark of the silicified stems within this mass in some cases have been converted into lignite. Shafts have been sunk in many places but usually only black shale has been found. At one place, 37 inches of such shale with much coal was found. The Leakesville deposit is insignificant and its area is but a few square rods.

Triassic rocks are exposed in very many localities west from the 105th meridian to the coast but they appear to be without coal in both the United States and in the Dominion of Canada.

Mexico.—But coal is present in Triassic deposits of the Santa Clara field on the eastern border of Sonora, Mexico. Dumble⁴⁶ has given brief notes respecting the locality. The Rhætic age of the deposits was recognized by Newberry and Fontaine after study of the plant remains. The region has been disturbed greatly by igneous rocks, which have metamorphosed the coals. The heavier sandstones are uniform and are moderately coarse conglomerate grits, which have a few fragments of silicified wood and occasional imprints of stems. The shales and finer sandstones are excessively

⁴⁶ E. T. Dumble, "Triassic Coal and Coke of Sonora, Mexico," *Bull. Geol. Soc. Amer.*, Vol. X., 1900, pp. 10-14.

variable, sandy shales change abruptly into coarse massive sandstone or into clay shale. The shales generally are rich in well-preserved remains of plants, which, according to Fontaine, are allied to those of Virginia and North Carolina. The more massive slates hold silicified stems and branches of shrubs, while the finer-grained sandstones have tree-trunks up to one foot diameter. No false bedding was observed in the sandstones.

Coal seams are numerous, each prominent slate bed having one or more; but in all cases these are irregular. Near San Marcial, southeast from the area of detailed examination, much work had been done on supposed anthracite, which proved to be only black slate; but at localities north and northwest from the mining center two seams are known, 8 and 10 feet thick. Much of the thicker beds is composed of coal with concentric structure, "shelling out into eggs of greater or less hardness."

The coal has been affected by the igneous rocks and usually it is a hard anthracite, though occasionally it is coke. In two important openings on the coke, igneous rock is the roof; in another, it is the floor; but other pits show no igneous rock anywhere near the coke. In one seam of anthracite, there are pockets of coke near the middle, while in a seam of coke pockets of anthracite were found at the bottom. In several beds divided by partings, coke prevails in some benches, anthracite in others. The proximate composition of the anthracite is: Water, 4 to 8; volatile, less than 5; fixed carbon, 76 to 85; ash, 4 to 8 per cent.

SOME CHEMICAL FEATURES OF THE COALS.

Coals of various grades are present in the Jura and Trias. Lignite and bituminous coal are present in the Lower Oölite of Great Britain within practically undisturbed rocks and at nearly the same horizon; while high-grade bituminous coal prevails in the Lias of Austria and Hungary, where the rocks have suffered severe disturbance. The Lower Lias of Siberia yields high-grade bituminous in the Tcheremkhovo and Grande-Bira fields but typical brown coal in the great Tchoulym region, where the strata are little disturbed and the rocks are only slightly consolidated. The Jura-

Triassic coals of Queensland are high-grade bituminous as are those from the Upper Trias of Austria and Virginia.

Cannel has been reported from the Jura of Alaska, but Collier saw none. Cannel, however, is certainly present in the Steierdorf-Anina field of the Hungarian Lias. Hantken has given the proximate analysis of two samples from the Hauptflötz, which show

Moisture	1.10	Volatile	53.77
	2.60		55.91
Ash	14.67	Fixed carbon	46.23
	22.00		44.09

The cannel is evidently in lenses, as at other localities this seam has only bituminous coal. In the same field, the Middle(?) Lias has a great mass of black shale, portions of which yield from 3 to 7 per cent. of crude oil, from which paraffin and illuminating oil are obtained. In Siberia the Lower Lias coal of the Angora River field is mostly of boghead type, while in the Ipswich or upper Jura-Trias of Queensland cannel or "oil coal" is present in a large area. Jack has given three analyses of the material:

	Ash.	Volatile.	Fixed Carbon.
Blackfellows Creek.....	17	56	43
Clifton, top seam.....	10	53	46
Clifton, lower seam.....	16	55	44

The seams at Clifton are separated by a considerable interval, which holds a seam of caking bituminous coal. Cannel prevails in the Walloon district where some of it is rich, that at Jimbour yielding about 37 gallons per ton.

The coals vary greatly in tendency to cake. Collier reports that none of the Alaska coals tested for him gives a coke. His samples, however, were collected mostly from outcrops, where leaching had been energetic during a long period. "Crop coal," even in the Connellsville region of southwest Pennsylvania, yields only a wretched coke. In Austria and Hungary many seams have caking coal but that from others is non-caking. In Siberia, the coals of the Tcheremkhovo and Grande-Bira fields are caking but that of the great Tchoulym field gives only pulverulent coke. The Jura-Trias coals of Queensland are caking in some instances, non-caking in

others. The Upper Trias coals of Austria are usually caking and those of the Richmond area are always so. Apparently no relation exists between proximate composition and tendency to cake.

No reference to the presence of resins in coals of the Jura or Trias is made in any of the works to which the writer has had access. One observation by Witham, cited by Miller, bears upon the subject. In studying silicified stems of *Pinus eiggensis* from the Lower Oölite of Scotland, he discovered that the wood abounds in turpentine vessels or lacunæ, well defined and varying in size.

Mineral charcoal (Fusain, Faserkohle) is a characteristic feature throughout. At times, it forms thin partings in seams, but at others it is an important constituent of thicker partings, where its abundance suggests that the partings are merely residues from a considerable mass of peat. Occasionally it is in lumps, embedded in the coal or in a clay parting.

Sphærosiderite or clay ironstone is reported by all except a very few observers. It is present in the coal, in the underclays, and is scattered in the other rocks, while occasionally it is in layers of varying thickness. At times, it replaces the stems of trees or fragments of wood. Black band layers, associated with seams of coal, have been reported from the Ipswich formation of Queensland and from the Rhætic of North Carolina.

The Jurassic coals of Great Britain are lignite or very low grade bituminous. No analysis of the coals in France is available. The analyses of the Austrian coals, as officially given, are incomplete and afford no information for comparisons; but the coals are clearly high grade bituminous, for that of many seams is caking. Hantken has published many analyses of the Jurassic coals in the Steierdorf-Anina and Fünfkirchen areas, and Nendtwich made a number at a much earlier date. The Steierdorf-Anina samples have as proximate composition:

The low percentage of ash makes evident that the analyses are of specimens supposed to represent the average best coal from the mines. This, however, is unimportant here. The upper Liegendflötz is separated from the higher bed by about 300 feet of rock. No marked tendency to decrease of volatile downward is recognizable

	Water.	Ash.	Volatile.	Fixed Carbon.
Hangendflötz	1.94	1.72	33.77	66.23
	2.50	1.75	36.59	63.41
	1.55	3.10	32.47	67.53
Hauptflötz	1.74	1.28	35.04	64.96
	1.88	2.07	30.41	69.59
	2.10	7.26	39.94	61.06
	1.90	1.95	34.98	66.02
	1.70	2.21	30.22	67.78
I. Liegendflötz	2.25	2.56	32.23	67.77
	2.25	16.78	23.28	76.72
	2.25	2.56	29.22	70.78
	1.85	12.88	42.73	57.27
II. Liegendflötz	2.05	4.19	34.64	65.36
	1.85	3.44	30.77	69.23
	1.75	5.65	41.86	58.13

in this series. The samples from the lower seams, containing the high volatile, must be considered as consisting in part of cannel.

The analyses of the coals from the Fünfkirchen area, published by Hantken, are ultimate; reduced to pure coal, as were those from the Steierdorf area, they are:

Seam.	Water.	Ash.	Carbon.	Hydrogen.	Oxygen.
II.	1.50	24.93	89.6	4.5	5.8
IV.	1.10	13.03	81.6	4.3	14.0
VI.	1.10	5.10	88.1	4.6	7.2
XI.	1.58	7.80	91.7	4.3	3.9
XIV.	1.80	15.77	93.7	4.5	1.7
"	3.20	11.64	77.7	4.7	18.1
XVI.	1.00	13.67	93.4	4.6	1.9
"	5.44	7.28	85.7	4.3	9.8
XXIII.	1.60	15.45	82.9	4.2	12.8
XXIV.	2.70	9.85	86.0	4.7	9.2

The order is ascending. The sulphur is from 1.07 to 6.88 per cent.; but in the great mass of seams XI. and XII. it does not exceed 2.50. In IV. at Vasas there is but 1.23 but at the Colonie mine it is 6.88. The thickness of the seam and the proportion of sulphur are not in relation; some thin beds have little, others much. The coal of XII. yields a great quantity of illuminating gas, that from three other seams about two thirds as much, while that from others is much less. The two analyses for XIV. and for XVI. are from different localities, but only a short distance apart. The local conditions

differ little but the oxygen-content at Szabolcs is very much greater than at Colonie. The proportion of oxygen has apparently no relation to the depth below the surface.

The analyses by Nendtwich⁴⁷ show as a rule less ash in the Steierdorf coals than in those of Fünfkirchen but the oxygen is somewhat less.

The Lower Jurassic coals of Siberia, according to analyses given by the Comité géologique, show extreme contrasts. I. and II. are from the Tchoulym field and III. is from the Grande-Bira area.

	Water.	Ash.	Carbon.	Hydrogen.	Oxygen.
I.....	11.68	1.56	69.92	6.13	23.95
II.....	16.66	2.28	69.73	7.12	23.15
III.....	2.35	12.00	81.8	5.5	12.7

The brown coal obtained in other districts is much inferior, as ash is very high.

The Jura-Trias coals of Queensland are bituminous throughout. Jack reports only proximate analyses but these suffice to show the great difference in conditions :

IPSWICH GROUP.

	Water.	Ash.	Volatile.	Fixed Carbon.
I.....	1.00	24.35	32.42	67.57
II.....		19.00	27.7	72.2
III.....	1.32	31.61	29.3	70.6
IV.....	2.02	22.8	30.8	69.1
V.....	1.32	19.70	29.3	70.6
VI.....	8.10	2.50	43.29	56.70
VII.....		16.00	42.81	57.1

BURRUM GROUP.

	Water.	Ash.	Volatile.	Fixed Carbon.
I.....	2.50	2.50	32.00	68.00
II.....	2.00	8.00	31.25	68.75
III.....	2.25	2.10	30.47	69.53
IV.....	2.75	3.25	29.50	70.50

The Ipswich coals throughout are very high in ash, the specimen VI. being picked from a thin band; all the coals except VI. and

⁴⁷ C. M. Nendtwich, "Ungarns Steinkohlen, etc.," *Haidinger's Berichten*, Band IV., 1848, pp. 18, 21, 30.

VII. are coking; the high volatile in these last, so greatly beyond that of other coals within the same little area, suggests that perhaps they contain some cannel. The Burrum specimens are all from a very small area, where mining has been carried on extensively and they are from only two seams. II. and III. are from the bottom and top of the Lapham or most important seam. The ash is low throughout, showing that, in this area at least, the conditions were favorable to the accumulation of clean coal. All of the seams yield good caking coal, though they differ in the hardness; that from several seams is hard shipping coal whereas that from others, especially that from one, is tender and therefore inferior as a steam coal. There is nothing in the structure to explain this difference as the seams are separated by a small interval. The Lapham coal yields 10,200 cubic feet of gas per ton, with 14.73 candle power; this is the result of a trial lasting for 20 months.

The Triassic coal of Norroy, France, was analyzed by Regnault, who obtained 19.20 per cent. of ash. The ultimate composition of the pure coal is: Carbon, 77.23, hydrogen, 5.39, oxygen and nitrogen, 17.37. Servier asserts that the specimen was not fairly representative and gives the results of a proximate analysis by himself: Moisture, 10.00, ash, 9.20, volatile, 42.4, fixed carbon, 57.5. This he regards as a fair average composition. He thinks it is a transition from brown to stone coal but the distillate is alkaline, not acid.

The Upper Triassic coals of the Richmond basin are all of high-grade bituminous quality, are caking and for many years they were used in the manufacture of illuminating gas in New York, Philadelphia and other large cities. The available analyses are those reported by W. B. Rogers,⁴⁸ which represent the average of the coal as observed at the more important localities. Twenty-two analyses were made. The ash is below 6 per cent. in all except 7 and exceeds 11 per cent. in only 3. The volatile in pure coal varies from 30 to 40 per cent., south from James River, and from 25 to 35 in mines north from that river. Much of the basin is broken by dikes which in some portions have converted the coal into coke; but there are anomalies not due to the influence of igneous rock. Analyses of samples from the bottom, middle and top of the thick

⁴⁸ W. B. Rogers, "Report of Progress for 1840," reprints, pp. 532-535.

mass in one shaft show 40, 30 and 31.7 per cent. of volatile in the pure coal, with 10.82, 5.10 and 9.52 of ash. In a shaft, north from James River, the 4 divisions of the coal show a difference of about 4 per cent. in volatile, while the ash is 5.20, 22.20, 9.80 and 22.60 in the several divisions.

Stone, in his report already cited, has given analyses of the coal at Leakesville in the Dan River area of North Carolina. The seam is an insignificant lens but is apparently the most important deposit in that area. It is in two benches separated by only 2 feet of micaceous shale but the composition is very different. The

	Water.	Ash.	Volatile.	Fixed Carbon.
Upper bench.....	11.67	9.65	38.6	61.3
Lower bench.....	5.35	20.27	12.8	87.1

lower bench is anthracitic and the upper bench is a high-grade bituminous. The sulphur in both is at most little more than a half of one per cent. The ash is very much higher at most of the North Carolina localities, occasionally reaching 39 per cent. in "best coal."

It may be well to gather the notes respecting ash as presented in the several analyses. The conclusions at best can be merely tentative because analyses, in almost all cases, appear to have been those of hand specimens supposed to represent the average of the seam as shipped: and there are comparatively few showing the composition of coals not regarded as fit for working. It is sufficiently clear that conditions were not the same in all portions of the area occupied by any seam or during the time of its accumulation.

In the Jurassic region of Austria, the coal of one seam near Bernreuth, though externally resembling good coal, has 42 per cent.; near Gresten, the same seam has only 3.9 per cent. The ash is low at Hinterholtz but at Grossau it rises to 10 per cent. At Pechgraben the average of all analyses is 17. These in all cases are from coals which are mined. No attention was paid to other seams because they are "dirty." Similar conditions exist in the Triassic region of Austria. Near Kleinzell, the highest seam has 14 per cent.; near Lilienfeld, the good coal, with little more than 7 of ash, is in the middle seam; near Kirchberg, the coal mined has from

15.8 to 19.9 of ash; but near Rehgarten, the same beds yield a coal, with only 7.8 per cent. of ash; at Loichgraben, the lower seam has good coal, while that from the upper seam, though in appearance equally good, has 52 per cent. Coal is mined near Gossburg, which contains upwards of 30 per cent. of ash. Rachoy has shown clearly that in both Jura and Trias a seam varies greatly in this respect in different portions of its area.

There are numerous coal seams in the Steierdorf-Anina area of Hungary, but only 5 of them are workable—each of these in limited spaces. They are divided into benches, some containing good coal, the others worthless. Samples of good coal from the highest two have from 1.28 to 7.26 of ash, while those from the third have from 2.56 to 16.78. The fourth seam shows less variation, the percentage being 3.44 to 5.65. Within the Fünfkirchen region, 174 seams were crossed by the tunnel at Vasas, with a total thickness of 52 meters. Thirty-nine of them, 14 meters thick, are “dirty” and worthless; of the 28 seams, which are workable in areas, large or small, at least one third become at times too impure to be mined. Hantken gives 26 analyses; 5 show between 16 and 20; 7, from 12 to 15; 4, from 10 to 12 and only 5 have less than 6 per cent. of ash. All of these are from mines in full operation.

The brown coal of the Tchoulym field in Siberia has at most only 2.28 of ash in the samples analyzed but, apparently, the same horizons in the North Tchoulym area yield coal with more than 30 per cent.

The Ipswich seams of Queensland have from 19 to 31 per cent. of ash, while the Burrum coals are all remarkably free from mineral matter, the highest percentage being only 8.

The analyses of specimens from the two benches of a coal seam in the Dan River district of North Carolina show 9.65 in the upper bench and 20.27 in the lower. The best coal in the area has only 5 to 6 per cent., but other samples of “best coal” contain from 20 to 39 per cent. Samples taken by the early students in the Richmond basin were all from the mines then in operation. The lower division of the great seam is usually described as much inferior to the higher portions. In most cases, the samples appear to have been chosen from the better portions, for the ash rarely exceeds

5 per cent.; but in two mines the samples represent different parts of the great seam and the contrast in conditions is marked; at one mine, the ash content in the several parts is, ascending, 10.82, 5.10 and 9.52; in another, the percentages are 5.20, 22.20, 9.80 and 22.60.

There is little of detailed information respecting variations of coal in different portions of lenses, as analyses have been made only of coals supposed to be worth mining. But incidental references abound, which show that, toward the borders, ash increases until the coal becomes worthless.

SUMMARY.

The areas of Jura and Trias, containing coal in economic quantity, are utterly insignificant, when compared with those in which the systems are exposed; but there are many localities in which coal accumulated during brief periods and amid unfavorable conditions. The oölite coals of Britain and a few spots on the continent of Europe are of inferior quality, merely local and almost without interest. Elsewhere the useful deposits are in the lower part of the Lias and in the highest divisions of the Trias. The Jurassic above the Lias and the Triassic below the Keuper may be regarded as barren.

The associated rocks are as in the later periods. The Oölite coals of England are intercalated in sands; the Jurassic coal of Spitzbergen is confined to the Middle or sandstone division, as defined by Nathorst; the Grestener or coal-bearing Lias of Austria is composed of sandstones and clays; the same conditions prevail in the Liassic coal areas of Hungary and Siberia; the Jura-Trias of Queensland and New South Wales are almost wholly sandstone; the upper Trias in Austria and Hungary is sandstone with intercalated shale. But the Jura in Alaska is almost wholly shale and the Upper Trias in some small areas has little sandstone. Freshwater fossils, in rocks associated with coal seams, have been observed in England, Siberia, Spitzbergen, France and Queensland. The structure of the rocks is evidence of, at most, shallow water and in some cases it is very suggestive of eolian agency. False bedding is reported from England, Australia, Germany and North Carolina and ripple marks

are common features at many places. Sandstones and shales frequently contain logs of wood, in such relations as to leave little room for doubt that they are simply stranded material.

There is, however, ample proof that the sea invaded many places where coal was accumulating. The Lower Oölite of England has beds with great abundance of fragmentary marine shells; the Liassic sandstone of Austria and Hungary includes layers with many marine mollusks of littoral types; *Ammonites* was found at one locality, but that does not militate against the conclusion that the water was shallow—if the shell be not drifted, it shows that the genus could exist in shallow water; the Rhætic of Sweden is freshwater below, but has marine shells in the upper portion, where the coal seams are very thin and impure. The lower beds of the Jura-Trias in Queensland have yielded a few specimens of offshore mollusks. The incidental references to beds with marine fossils do not enable one to determine the extent of areas covered at one time or another by salt or brackish water; but in the Fünfkirchen district of Hungary such beds, though few in number, are present in the roof, floor or even partings of several coal seams, recalling the conditions observed in southwestern Utah, within the Benton, near base of the Upper Cretaceous, where a coal seam between beds of marine limestone has freshwater mollusks in a parting. In any event, these deposits suggest that the areas in which they exist were lowland, close to the ocean level. The shallowness of the water cover during their deposition is so evident that one may well conceive that the invasions were due to diversions of drainage, to shifting of channels of large streams. How readily such shifting of channel ways may change conditions in a plain country is shown by Featherstonhaugh's⁴⁹ statement that, in one area, the Arkansas River broke through its banks and converted 30,000 acres into swamp land, killing all the trees. Still more remarkable illustrations exist on the broad plains bordering the Paraguay and other rivers in South America. Many times in sections of coal-bearing rocks, marine deposits are in contact with those of land origin or are separated from them by an inch or two of fine sediment.

⁴⁹ G. W. Featherstonhaugh, "Geological Report of Examination of the Elevated Country between Missouri and Red Rivers," Washington, 1835, p. 84.

The lenticular form of coal seams is as distinct in the Jura and Trias as it is in later periods. It is characteristic of Jurassic coals in Great Britain, France, Austria, Hungary, Siberia and Queensland, as well as of Triassic coals in France, Austria and the United States. Direct reference to this feature is not made in some of the earlier reports as, at the time the studies were made, the bearing which the form of coal seams has upon the problem of their origin was not recognized. But in every area the varying thickness of coal seams is emphasized; the frequent passage of coal into carbonaceous shale is noted; the presence of coal seams in some vertical sections and their absence from others attracted the attention of all observers. The lenses may have considerable area but often they are small; they may be thick or thin. Those of the Tchoulym field of Siberia have small superficial extent, rarely exceeding a few square kilometers and they are rarely connected, but their thickness is so great that the Russian geologists speak of the total quantity of coal in this district as "colossal."

References to contemporary erosion are rare in the reports. Wilkinson has recorded instances of filled channel ways in the Triassic of New South Wales and Hertle has described an interesting "horseback" in a Triassic seam near Rehgarten in Austria. The irregularities in the roof of coal seams in the Richmond field, as described by several observers, have much resemblance to "horsebacks," but the mines in which they were seen were abandoned half a century ago, so that one cannot determine whether or not these irregularities are due to trenching of the coal seams.

Soils of vegetation have been reported from England and the United States, but, if they be present elsewhere as one should think probable, observers have failed to make note of them. In such soils one finds vertical stems of plants, rooted apparently in place of growth but not associated with seams of coal. The Purbeck "dirt beds" of southern England have stumps of conifers and cycads rooted in carbonaceous clay. Mantell states that the conifer stems have lost their bark and have a weatherbeaten surface like that of posts set between tides. They resemble the stumps exposed above the Yahtse gravels, as described by Russell. Stems of the Purbeck conifers were snapped off at 3 or 4 feet from the ground

and they lie prostrate in intervals between the rooted stumps. Henslow saw, at the Portland locality, root-shaped cavities descending into the rock underlying the dirt bed. Equisetiform plants in vertical position and rooted in place of growth occur at several horizons in the Lower Oölite and the Lias in Yorkshire. *Calamites* and *Equisetum*, in erect position, are found in beds above and below seams of coal at numerous localities within the Richmond field. These ancient soils, with erect stems in place, would seem to indicate land surfaces at various times during deposition of the coal-bearing deposits.

As in the newer formations, the roof may be sandstone, shale or limestone; it may contain marine or freshwater forms. At Brora in Scotland, it is a mass of marine shells with quartz sand and carbonaceous materials, bound together by a calcareous cement; it passes downward into coarse coal—a faux-toit. Marine shells are present in the roof of at least one seam in the Fünfkirchen district and bituminous limestone rests on the coal at some localities near St. Anton in Austria. The ordinary roof is sandstone or shale, one or the other predominating in different areas; not infrequently it is sandstone in one mine but shale in another nearby. Finely laminated sandstone is not rare. Roof shales are often very rich in plant remains, leaves being especially well-preserved, as though they had been lifted gently from the surface of the bog by muddy water. The sandstone roof of the Lettenkohle in Unterfranken is an old soil, containing erect roots.

Frequently, the passage from good coal to roof is gradual and this is equally true of the passage from coal to the floor, there being distinct faux-toit and faux-mur; but, at times, the passage is abrupt. Occasionally, the character of the coal changes in such manner as to suggest that one portion of the seam sank below drainage while the other remained above it; the "Kimmeridge coal" in the typical area is merely a rich carbonaceous shale, whereas in Wiltshire it resembles peat. In the Tchoulym field of Russia, the burial must have been abrupt, for the upper portion of the coal is very peat-like at some localities. Coal seams, more than 2 feet thick, are rarely single, but are divided into benches by partings of sandstone or clay, often containing much mineral charcoal. These vary much

in thickness. The interval between seams XI. and XII. in the Fünfkirchen area is from zero to 72 feet; similar, though less marked variations are recorded from other localities. Ordinarily, the partings appear to be of freshwater origin, but occasionally one contains marine forms of immediately offshore types. The character of the coal differs greatly, many times, in the several benches; some yield excellent coal, but that from others is worthless; that from one bench may be caking, that from another may be non-caking; that from one bench may be richly bituminous while that from another may be almost anthracitic. Coal of Jurassic and Triassic age is usually so far advanced in chemical change that identifiable plant structure seldom appears in the coal itself until after treatment with Schultze's solution. But Grand'Eury states that, at Nice, *Equisetites* is present in the coal, recognized by its form, though all trace of structure had disappeared. The Keuper coals of the Vosges contain bark and seeds, while Rhætic coal from Bayreuth has many streaks which appear to consist wholly of pollen exines. In the Rhætic of the Richmond field *Equisetum* is abundant in coarse coal. But treatment with Schultze's solution brings out evidence of vegetable tissue from all the coals examined.

The floor is as variable as the roof, being clay, shale or sandstone. Limestone is reported from only two localities described in works consulted by the writer. Within several counties of England the floor of the Lower Oölite coal or coaly shale is usually clay or fine-grained more or less clayey sandstone and it contains many roots, which, in at least one locality, clearly descend from the overlying coaly shale. A calcareous floor in the Causses of France holds roots, which are well defined. Lipold and his associates give no details respecting the floors of Austrian coal seams but the presence of plant remains is recorded incidentally for many localities. The presence of roots in floors is a familiar phenomenon in the Lias of Hungary; in the Steierdorf-Anina district, they are described as vertical, often branching, and they are associated with plants of several types. According to Grand'Eury, roots, both woody and herbaceous, are abundant in underclays and partings. The condition is similar in the Fünfkirchen area, where, according to Gothan, the underclay proved to be a root-bed in every locality

at which the floor could be studied. *Vertebraria* has been recognized in underclays of Queensland; *Equisetites* roots are in underclays of the Vosges as also at Nice, where the plants seem to have supplied material for the coal. The underclays of Lettenkohle in Unterfranken are root-beds. The coals of the Richmond field, according to Rogers, have nothing answering to the *Stigmara*-clays of the Carboniferous; but the underclays are present. They carry no *Stigmara*, for the gigantic *Lepidodendron* and *Sigillaria* had disappeared; but Fontaine has shown that *Schizoneura* is present in the floor of the main bed.

The flora has been studied in all of the important areas. In the Upper Oölite of southern England, ferns, conifers and cycads are the prevailing types; the Lower Oölite of Yorkshire contains ferns as the preëminent feature though conifers and cycads are abundant; *Equisetum* is common above the coal horizon, at which ferns and conifers prevail. Conifers, cycads and some ferns from Spitzbergen have been described by Nathorst. The Ipswich or upper division of the Queensland Jura-Trias has 11 species of ferns, 4 of cycads and one of *Equisetum*; ferns prevail in the lower portion of the Lias within the Steierdorf-Anina area and cycads in the upper; but in the Fünfkirchen area, the flora consists chiefly of ferns, cycads and lycopods. *Equisetum* is extremely abundant in the Trias of Austria and *Calamites* and *Pterophyllum* were obtained at many places; the Trias of Hungary has yielded cycads, *Palissya* and some ferns, but collections have been small, as the coal is unimportant. The beds in the Atlantic coast areas of the United States contain cycads, reeds and ferns—the last being few in species but extremely abundant in individuals.

That the coal-bearing deposits were laid down on an undulating surface is well shown in the Liassic areas of Hungary. Within the Törzburg area, the underlying rock is crystalline schist; in the Steierdorf area it is Dyas but in that of Fünfkirchen it is Trias. A similar condition is distinct in the Trias of Virginia and North Carolina. In the Richmond field, the interval between the lowest coal seam and the granite varies from a few inches to 600 feet, while in the Dan River basin of North Carolina it is more than 1,000 feet.

THE ARCHÆOLOGICAL SIGNIFICANCE OF AN ANCIENT DUNE.

By CHARLES C. ABBOTT, M.D.

(Read December 7, 1917.)

When solid rock is before us, its history is readily traced, its place in geological sequence determined and its characteristics, lithological and mineralogical, determined beyond dispute, but, when this and associated rocks are reduced to a coarse powder or sand and carried by water or borne by wind hither and yon, it is with difficulty that the earlier chapters of the record of its career can be deciphered. As words accumulate as books due to the winds of doctrine, so, ridges, hillocks and undulating plains are formed when the wind gains access to the sand and rearranges the same *en masse* as the stable fixtures of the region determine. These are transient, necessarily, every shifting of the wind changing the scenery, but traces of some of these phenomena have, by lucky chance, survived every vicissitude and it is possible to discover what remains of a one-time dune that was shaped by the winds blowing over a desert-like plain, and at a time when the ocean water filled the adjacent river valley and the tributary brooks were filled with brackish water due to the inflowing tide, and this at a point now fifty miles inland.

In other words, here in the valley of the Delaware River, at the head of tide water, but where the salt or brackish water now never reaches, is what remains of a dune that formed on the bank of a small creek, now diminished to a brook that itself is reduced almost to the vanishing point during the drought of mid-summer, but has been known to resume its former importance as the result of a cloudburst or of a protracted but less impetuous rainfall.

So changed now are all the conditions of a few thousands of years ago, that it seems hopeless to reconstruct the surrounding country at the time the dune was formed. This is a task, however,

that should never be beyond the capabilities of an archæologist. Such reconstruction is not a side-stepping from facts to fancy, but a confirmatory demonstration relating to the discovery of artifacts.

The plat under consideration is the low-lying termination of a long, rectangular field, mostly at a considerable elevation above the brook that drains a tortuous valley of about five hundred acres. The "dune" area is not distinguishable, at present, from the field of which it forms a part, but until recently was noticeable because of a slight conical elevation, which was the more prominent when not covered with vegetation. The surface soil is a shade lighter than that of the field of which it is a continuation and of finer grain, as indicated by clouds of dust that rise from it when a breeze passes, but which is not forceful enough to equally affect the surrounding surfaces.

This plat, the "dune," if such it be, was deforested about 1770 and since 1800 has been more or less continuously under cultivation. The region hereabout, a plain of thousands of acres, has undergone marked changes since the influx of European settlers, less than three centuries ago. Before that time, it was distinctly one of hills and hollows that have now disappeared. Lands deeded as "swamp" and "meadows" have now lost every vestige of such conditions as these names imply, and only a slightly undulating surface marks what was once highly diversified. This change is due, unquestionably, to deforesting and subsequent cultivation, for a sandy soil, unprotected by vegetation, is necessarily the sport of the elements. Wind and rain attack it viciously at times or playfully, if we may so call it, but the surface is affected by the lightest breeze and the gentlest rain. I have known a strong March wind in seventy-two hours to build up a ridge of sand, a hundred yards long, twelve yards wide and seven feet high; leaving a depression in an adjoining field, from whence the sand was carried deeper by the subtraction of this "dune," of about sixty thousand cubic feet. Again, on August 24, 1877, there was a "cloudburst" here that materially altered the surface in places, although practically all the area was protected by growing crops or weeds, yet tons of sand and gravel were washed from upland fields and carried to the meadows, and a gully through which the present brook flows—the natural out-

let for ordinary drainage—was deepened until the clay underlying the coarse glacial gravel was exposed. The ordinary rains of a season falling on ploughed ground may not have a marked effect, but the rains of centuries tell another story.

A section of this dune, cut to a depth of about six feet, shows the present surface soil of about eight inches and of a brownish color inclining to yellow, and beneath, a thick deposit of yellow sand, or brownish-yellow, which is very compact, of uniform size of grains and without any trace of stratification. This, more than aught else, suggests that it is a wind-blown deposit from some near-by point and subsequently compacted by pressure of an overlying stratum and the slow infiltration of moisture.

This deposit, during severe winters, is frozen, nearly if not quite, its whole depth, but this and the subsequent disappearance of frost does not affect its structure, except to gradually render it more compact.

This yellow sand is but a continuation of the present surface soil, the difference in color being due to stain from the yearly coating of broadcasted barnyard manure and the decomposition of vegetation.

The deposit merges into a greenish sand, of somewhat coarser grain and looser texture, which in turn rests upon coarse gravel and this on the clay—possibly pre-glacial.

This uniform structure of the deposits is not confined to the entire area or the conical hill to which reference has been made. Near the center of it we meet with irregular bands of red clay of varying thickness and of more varying length. This clay is in no sense a continuous deposit of this material as when the Raritan or Pensauken clays were laid down, nor are they derived directly from them. I should say they are due to gradual infiltration when the texture was looser than at present and so a deposit of argillaceous character from overlying sand and the actual surface carried to where the more compact sand checked the water—summer rains and melting snows—and the particles held in suspension were arrested. This once started, the water would be held here, later, until all foreign matter was deposited. Even now, there is very little sand to be found here, that is even approximately clean, and the sand of this

dune clouds the water when thrown into it. This method of band-formation is beautifully shown, where extensive exposures, *i. e.*, of hundreds of square feet, have been made. Deep-lying bands can here be directly connected with the surface, the lines or channels of infiltration or inflowing still to be seen.

Sand is never found where it originated as sand. It is, from the day of its origin, a wanderer until conditions finally imprison it, as with this dune, which was derived from the surrounding area, whether wind or water left it where it is. This, of course, necessitates an open country, for the wind cannot reach the sand when protected by vegetation. It was an open country and a coastal plain in a very literal sense, and it was such at so remote a date, not geologically, but as we measure history, that the water of the brook nearby was salt or brackish, as evidenced by the presence of a marine conchological fauna—*Mya*, *Ostrea*, *Cardium*, and undeterminable fragments. Also four valves, broken, of an *Anadonta* or *Unio* ———; all of which brings us face to face with an antiquity worthy of consideration, as there is also an archæological interest in this dune, in that it contains traces of man's handicraft.

Or, are these traces of man, intrusive objects? The plat under consideration was part of an extensive forest less than two centuries ago; the tree-growth being largely oak, with some chestnut, maple, birch, sour gum, hickory and sassafras. The undergrowth was largely greenbriar (*Smilax rotundifolia*), with some ampelopsis and grape. The ordinary semi-aquatic growths of to-day fringed the brook and in such effective fashion that the water was hidden except in winter.

The annual deposit due to decay of such vegetation is greater than the erosion and has therefore gradually raised the surface of the brook's surroundings; not measurably perhaps, but certainly to some extent during many centuries. That at one time there was an open brook with characteristic fauna is certain, as even now, when the stream is at freshet stage, the mud minnow (*Umba pygmosa*) and crayfish (*Cambarus diogenes*) come from the reaches of the brook nearer the river, where the conditions for aquatic life are favorable throughout the year. It is, however, the one-time tree-growth to which attention should be called, and not

without reason, particularly to the oaks. These are of slow growth, yet reach to the largest dimensions. It is within a short distance from this dune that, until 1869, there stood a white oak (*Quercus alba*) which was twenty-seven feet in circumference, three feet from the ground. It was, unquestionably, at least one thousand years old,¹ but we have no warrant for assuming that this ancient tree was the ancestor of all the white oaks. On the contrary, this forest, when at last felled by the settlers, who sacrificed all beauty to their god, utility, was the remote descendant of a primeval forest growth which began to flourish who shall say when?

If this locally known "Pearson Oak" was the remote descendant, as is logically certain, of *Quercus* I. of the reign of Oaks, or the last of a long line of forest monarchs, then we must ascribe to the forest floor or that soil which in slow course of time accumulated during the period that the "dune" and its surroundings were forested, an antiquity which removes it from the remotely historic to a strictly pre-historic time.

I know of no means of determining when the forest age was ushered in, except that we view it from the point of physical geography, if not really a geological standpoint. The forest growth would not start until the condition of soil was favorable, and, in this instance, a change from a coast-line condition to an inland one and strictly fresh-water upland, quite uninfluenced by the ocean tides. How long then was this change in taking place? Also, when, while an herbaceous flora was in its prime, did tree-growth begin? Was it not until the lesser, annual growths had flourished long enough to spread a thin soil due to decomposed vegetation over the old "dune"? Grasses, more pretentious flowering plants, permanent shrubbery, might well have had a long day of their own, before the overshadowing tree-growth began to encroach on their domain, and there is not a particle of evidence forthcoming that the reign of oaks was not a period of several thousand years.

The result of the forest growth is the formation of "black soil," as it was called by Peter Kalm,² and how long it took a foot or more of it to accumulate is problematical. It was never a period of wholly

¹ See Annual Report, Smithsonian Institution, 1876, p. 260.

² "Travels into North America," London, 1770, Vol. II., p. 19.

undisturbed accumulation. Through every woodland tract there trickles a little brook, and often a stream of considerable width and depth broke the monotony of a forest floor. These would necessarily prevent a uniform accumulation of each season's foliage, a large proportion being carried away, for I have often seen currents of air lift and bear away the dead leaves in a forest and deposit them far from the trees from which they fell. Matted dead leaves are bulky, but when such leaves have lost their identity and become dust, the result is an addition to the accumulating soil not thicker than a sheet of tissue paper. Adding to this the decay of fallen tree trunks, we must still admit that the growth of a forest's black soil is a matter of centuries; that it is one of Nature's slow processes. It was on this floor that the Lenni Lenape dwelt, and for how many generations I think no one will presume to deal in figures. He came and little do we know of his career, save that it was not one of such bestial savagery as has been asserted. The variety of artifacts fashioned by him is evidence of this.

When, in 1678-80, the English settlers began in grim earnest to convert the wilderness into a garden, or destroy beauty in the interests of utility, the forest floor began rapidly to disappear. Where the surface is undulating, and I have seen but slight acreage that might be called "a dead level," the forest floor, when exposed to the weather, is washed or blown off and not worked or washed into the underlying sand. The result of rain, if not violent, is to compact sand and steadily lessen its penetrability. This leads us to a consideration of the suggestion, so frequently made, of the intrusion of objects from the surface: that a grooved axe or polished celt or broken pot or other distinctly "Indian" possession had by chance sunk from the surface where it was lost or intentionally left and reached to a considerable depth in the yellow sands beneath and since its passage, all trace of the track of its intrusion become obliterated. Such disturbance always leaves behind it ineradicable traces. The yellow sands, whether laid down by wind or water action, become arranged in such a way that, if disturbed, no rearrangement on the same lines is practicable. Those who have trenched in such deposits intelligently known instantly when a spot has been disturbed since the original deposition. Nature has not

the power to repair the damage so that it can deceive the observant eye and skilled hand of the experienced archæologist. When a "foreign" object is discovered in the yellow sands, it is recognized at once as part and parcel of the containing bed. If, again, intrusion were possible, why is not pottery found at all depths to which undoubted artifacts occur? Why not the familiar surface finds that collectively we call "Indian relics"? I have gathered probably fifty thousand such objects, and have lingered so long over sand banks and gravel beds that I feel entire confidence in the message they hold out to me, and this intimate association has a significance that is not within the experience of the casual observer, who too frequently is the victim of preconceived ideas. To decipher a sand-bank requires patient labor and constant association and, above all, endless comparisons of one point of view with another. Without this, the digging of a single trench and the gathering of a few score "traces" of man's presence is what the hint is to a practical demonstration. Unfortunately the hint has often led to the most grotesque conclusions, and the fact of man's antiquity been hidden by an array of assertions to the contrary, not one of which has an iota of warrant. I assert without fear of successful contradiction that "Indian" relics do not occur in the yellow sands underlying the forest floor.

The character of the disappearance of the forest floor by rain-wash or wind at once demonstrates that such traces of a people who were forest-dwellers as stone artifacts and pottery would ultimately be left scattered over the surface of the underlying formation, upon which the forest floor had been built up. The greater part of such traces, as axes, celts, spear-points, steatite vessels and pottery would prove too heavy for the gentle action of rain or wind, and *a storm's cataclysmic action would only bury such objects with abundant evidence of how they were buried, so no confusion need arise.* As it is, we find, on the one hand, the relics of the historic Indian with traces of the country's Colonial period, and, on the other, with such traces of the precursor of this forest-dweller as were left upon the surface of the ground when the forest floor began to accumulate, or earlier. No one hesitates to separate the pennies of the English kings from Indian arrow-points, although found together; but upon what basis,

we are asked, is a distinction to be drawn between a chalcedony knife or elaborate gorget and a rude basalt or argillite point with which it is now associated? It has been denied that any such distinction could be drawn and it is curious and significant to know that the vehemence of this insistence is in direct proportion to ignorance of the locality. The conditions that here obtain are favorable to preservation of traces of the sequence of events; very generally they are absent.

To eliminate doubt, when a trench is opened, or where any digging is done, other than systematic trenching, the present surface—in no sense an “Indian” surface—for a reasonable depth is not admitted to be demonstrative as to the age or origin of the artifacts found therein. This zone of doubt I have considered to be the topmost six inches, after removal of the twelve inches of surface that has been continually disturbed by cultivation. Assuming the forest floor to have been twelve inches thick—I have found it considerably more in some localities—then an artifact found some ten inches below the zone of doubt would have been forty inches below the surface if the forest floor still existed. When, then, we consider that this dune, treated by others, as well as by myself, at different points, have exposed pebbles, and some too large to suggest eolian origin as to locality, shells, marine and fresh-water, fragments of bone and artificially produced chips of basalt and argillite, and a few of chert, and completed artifacts.

In my own experience, the position of every object, as exposed, suggested—demonstrated?—that it had not slipped down any crevice, but always with the long axis of its diameter horizontal. This, I believe, is the experience of those who have examined the deposit. Several long, narrow points of basalt or argillite have been recovered and every one was as described, as to position; the deposit suggesting, by reason thereof, water action and the points floated or rolled to their position when found. However this may be, the fact remains, that the dune, assumed to be post-glacial, has a geological antiquity and that it contains traces of man that reach back to the time of its formation.

A few words in conclusion concerning the sand deposits of the neighborhood. As familiar to all, the unimpressionable rock is our

standard of stability and its opposite, the so-called, ever-shifting sands. It is to be noted, however, that extremes are always giving rise to misleading impressions. Rocks are not so resistant as to merit the term "eternal" and many a bed of sand has withstood the changes that time has wrought about them for unnumbered centuries. This has not been duly considered by those geologists who feel at home among the rocks where Nature presents a decipherable script, but omits it where only sand has been accumulated. Because of this extra demand for exertion in solving geological problems, the natural history of sand has been neglected or grotesquely misrepresented.

There is a wide distinction between quick-sand, dunes, and the long level reaches of a sand deposit due to aqueous and not eolian transporting force, that has been shut from the light of day and little affected by the rain that reaches it or frost that penetrates the earth's mat sufficiently to congeal its moisture. There is, too, a vast difference between a sand that has been washed until nearly pure silica and sand with sufficient clay to produce a more or less marked cementation of the mass. Hence it follows that there is a great difference in degree as to the penetrability of a deposit of sand, the clay rendering it resistant in proportion to its presence.

Having considered the dune as such and derived from the immediately adjoining fields, the archæological interest now shifts to a locality about nine hundred yards west of the dune and trenches opened by Messrs. Skinner and Spier. There is in this locality an area of some one thousand acres where sand underlies the present surface soil. It varies considerably, as sand, and suggests that since the original deposition it has had a varied experience, the same agencies not affecting the whole area. Thus, it has given rise to various opinions as to its age and origin, the judgment based upon a single point of examination. That this sand area was at one time the sandy bottom of a shallow arm of the sea is probably true, if not demonstrably so, as I believe, and so gives a clue to the age of the artifacts contained therein; the sequence of event being—as suggested by the late Prof. N. H. Winchell, after an examination of the locality with Mr. Volk and myself, Aug., 1913, and this suggestion he maintained with greater confidence after an exhaustive study of arti-

facts from here, surface-found, from the sands and from the implement-bearing drift gravels, declaring that the changes wrought in the surfaces of these worked stones could only be explained by long submergence in sea water.³

Illustrative of this, July 4, Mr. Albert Moyer, of New York City, and myself, made a section of these sands, and he had the good fortune to expose, by careful paring down of the exposure, a series of objects, all of which are, I think, of artificial origin. The surface soil, twelve inches in depth, was carefully removed and the sand underlying for several inches was considered a zone of doubt and nothing found therein was accepted as indicative of antiquity. Beneath this, the sand was of lighter color, and only moderately compact, but increased in density and where really resistant to the trenching tool, the artifacts were found. Among them was a minute fragment of pottery. This was a little disconcerting, for I have never seen potsherds from these sands and Mr. Volk informs me, he has never, in his many years' experience, found any traces of pottery, even of the rudest pattern. I can only conclude that pre-Wisconsin man was acquainted with the rudiments of the ceramic art.

Probably more effective than rain in changing the conditions of a deposit of sand is the action of frost upon it. This, of course, refers to rain as absorbed and not as a transporting agency. I have known the soil and sand at this point to be frozen to a depth of four feet, while the lowermost of the artifacts found by Mr. Moyer was forty inches below the surface and twenty-two in the compact, undisturbed, clay-cemented sand, so it becomes evident that during many winters of each century since the sand was in its present position and under present conditions, these objects have been frost-bound and then liberated by the springtide warmth. This periodic condition of frost appears only to affect physically but not disturb or displace the containing bed. The upheaval of the surface of a field is only soil deep in its disturbance of the contained pebbles and artifacts. They may be lifted up and let down, but the relative position of these objects, each to the other, is not materially changed

³ See Winchell-Abbott Correspondence—unpublished—at Peabody Museum, Cambridge, Mass.

and there is no significant inhumation of a surface-lying specimen. A notable example of this non-disturbance is shown in caches of chert or basalt blades, which have lain undisturbed near the surface, just as placed by aboriginal man, until cultivation of the soil or other interference by man brought them to light. Again, were frost an inhuming agent, how is it that stone mortars weighing from ten to fifty pounds do not gradually sink with each winter's freezing and thawing? I have passed over these relic-bearing fields when I sank "knee-deep" in the mud, but this pressure of the foot was a matter of twelve or fifteen inches actually and explained by the weight of my body, but a mortar or even a stone axe of five or six pounds ought *gradually* to sink deeper and deeper in sands when the frost has melted, but we never find them at any such depth as the lower compact sand of the "yellow drift," except perhaps in some deep pit, the definition of which is clearly shown by the dark discoloration and unmistakable boundary line. But, there, at such significant depth, we do find rude basalt and argillite artifacts of inconsiderable weight, usually less than an ounce, yet as distinctly the output of man's skill as the most elaborate production of the historic Lenape.

The single explanation of the presence of the characteristic artifacts of the yellow sands lies in the suggestion that they are as old as the containing bed and were made at the time or earlier than its deposition as now obtaining, be the agency of distribution either wind or water. That these traces of early man are intrusive objects is simply impossible, and this applies equally to the palæolithic implements of the Kansas gravel, through which the Wisconsin Ice-age floods have washed the present channel of the Delaware River.

AMERICAN SANITATION IN THE PHILIPPINES AND ITS INFLUENCE ON THE ORIENT.

(Read December 7, 1917.)

By VICTOR G. HEISER, M.D.

Sanitation is constantly becoming more exact. America's work in the tropics has contributed greatly to that end. The public is beginning to realize that science is rapidly reaching the point at which the proper expenditure of definite sums of money may be counted on to produce proportionate reductions in the morbidity and mortality rates. Every dollar wisely invested should produce an appreciable improvement. It does not necessarily follow that great sums of money are required. We are all aware of the marvelous results which were obtained by our health department in Panama. It is not so well known that equally striking results on a far greater scale were obtained in the Philippines. In Panama the cost has been given as approximately \$3.38 per capita per annum. In the Philippines the cost was about 20 cents, and the results were obtained under civil conditions without the use of military force or extraordinary powers. The entire cost of the sanitation was defrayed by the revenues of the Philippine government. When it is remembered that the Filipinos are among the lowest taxed people on earth, it will be apparent that it should be quite possible to achieve in countries with greater resources even better results than were accomplished in those far-away islands. Since my return to America it has been a great shock to me to find this country in many respects far behind in health accomplishment and to discover that sanitary procedures which have been in force and have been producing good results for many years in the Philippines are now only gradually coming into use and are being heralded as among the most modern and recent advances.

Soon after the occupation of the Philippines, a board of health was organized under Army General Orders No. 15, under the

authority of which army officers did good work and made an excellent beginning in reducing the ravages of certain diseases which they found very prevalent. This work was largely concerned with protecting the health of the troops and was chiefly confined to the city of Manila.

When the civil regime began, in addition to deplorable sanitary conditions resulting from centuries of neglect, the newly created civil board of health found itself confronted with a severe outbreak of plague in Manila and in a number of the provinces. To add to these difficulties, the board of health had scarcely opened its offices before there began one of the severest epidemics of cholera that has been known in modern times. In a little more than a year it numbered over 300,000 victims, of whom 150,000 or more died.

When the civil board of health began its work 40,000 persons were dying annually from smallpox. Beriberi in jails and public institutions was responsible for a large number of deaths. There was no governmental provision for the insane, and more than 3,000 of these unfortunate individuals were without adequate care. The sanitary condition of the prisons throughout the islands left much to be desired. With the exception of the water system which was available for a part of Manila, and possibly a few other minor installations, there was not a reservoir, pipe line, or artesian well for the seven or eight million people of the entire archipelago, and even the water for Manila was known to be grossly polluted. The burial of the dead was not properly regulated. In making new interments, the bones of those who had been previously buried were frequently cast out to bleach in the sun or were thrown upon a bone pile. The city of Manila, with its population of over 200,000, had no sewer system. Disease-carrying human discharges found their way into esteros or canals or were deposited directly on the ground, causing serious soil pollution.

Sections of Manila varying in population from 5,000 to 25,000 were built up with houses so closely crowded together that there was no room for streets and alleys. Entrance and egress, in many instances, had to be made by passing under the houses. As most of these crowded sections were built over tidal flats, the difficulties of the situation can well be imagined.

There were no adequate building laws, and, as a result, too frequently the case in Oriental countries, small dark interiors with no light or air were the rule. Street cleaning was most indifferently carried out. Large quantities of garbage and other filth accumulated in the back yards and upon the streets. Tuberculosis was probably responsible for at least 50,000 deaths per annum, and no general education measures were in operation with a view to teaching the people how to combat disease.

There was no food law in the modern sense. Perishable provisions were sold under insanitary conditions. The vilest class of food products was often shipped into the country. There was practically no inspection of animals before slaughter, neither were there suitable slaughter-houses. Dysentery soon caused sad havoc among the American troops and among those who came in civil capacities. Subsequent investigation showed that the native population also suffered severely from this cause.

Hospitals for the masses, with modern operating rooms and surgical equipment, were practically unknown. Persons died on every hand with diseases which could have been relieved by ordinary medical procedures. It was not uncommon to find victims horribly deformed by conditions resulting from injuries or disease that could have been cured without deformity if skilled attention and facilities had been available in the beginning. There were perhaps a half million persons living in a wild state, for whom there was no medical relief.

In the days prior to American control, maritime quarantine was often conducted upon a basis of graft. Naturally the result of such lax methods was the introduction from nearby foreign countries of dangerous communicable diseases such as plague, cholera, and small-pox. More than 5,000 lepers were at large throughout the Philippine Islands. A few hundred were cared for by charity, but there was no attempt to segregate lepers with a view to avoiding the danger of infection or bringing the disease under control in the entire archipelago. Malaria, likewise, prevailed in hundreds of towns and there was no quinine with which to combat it. Imitation quinine pills were frequently sold at fabulous prices in the

stricken districts, and the people had no means of relief or redress from this intolerable condition.

It would be a pleasure to state that all the evil conditions mentioned above, as well as others, have been remedied, or relieved. This, however, is not the case. At best, in the time which has elapsed and with the funds available, it has been possible only to make a good beginning. Much ridicule was cast upon the efforts of the American government to better the sanitary conditions of an Oriental population. It had been a fairly well-established rule in other countries, in dealing with dependent peoples, to permit the masses to live as they would and to direct efforts at sanitation largely toward the benefit of Europeans. This policy, of course, was not in accordance with the views of the people of the United States, happily for the residents of the Philippine Islands, who are now enjoying most of the benefits available to the residents of Europe or America. The American sanitarian had much to learn, and in the beginning his efforts were further hampered by the passive opposition of the bulk of the population.

The first campaign against cholera was not as successful as could have been wished, but it paved the way to attacking future outbreaks with greater result. It soon became apparent that nothing was to be gained by the use of force. Methods of coöperation and of winning the confidence of the people were rapidly substituted for more drastic measures in controlling the disease. Early efforts to combat plague, also, did not meet with complete success, although better results were obtained than with cholera. In dealing with plague, not only Filipinos but Chinese and other races had to be considered. Efforts to bring the foreigners to the ways of the twentieth-century hygiene often would have been ridiculous had the outcome not been so tragic.

In brief, it may be stated that the American policy has been to bring about a sanitary regeneration of the Philippine Islands, not in spite of the Filipinos, but with their coöperation and assistance.

One of the first steps was to organize some 300 boards of health throughout the islands, with Filipinos in charge. In many cases the officials who composed these boards were brought to Manila and

given a course of instruction in modern sanitation and hygiene. This resulted in efficient coöperation. It is but natural that a people should resist health measures which they believe are enforced by the governing power for the purpose of making them miserable, unhappy, and uncomfortable. When it became apparent that cholera seldom occurred among Americans who drank only boiled water and ate only cooked food served hot, these practices soon had imitators among the better-class Filipinos and from them gradually spread to the masses.

Vaccination had been practiced in the Philippines for several centuries, but was never done in a systematic manner so as to reach all the population. The result was that a favorable soil for small-pox remained, and unvaccinated individuals were constantly attacked. Over 10,000,000 vaccinations were made in the Philippines, without the loss of a life or limb. As province after province fell into line, the disease disappeared in the wake of the vaccinators, so that the number of deaths was reduced from 40,000 per annum to a few hundreds.

The Island of Culion was set aside for a leper colony. The construction of a modern town was begun. When it had proceeded sufficiently far, the collection of lepers was started. More than 4,000 now find their home on the island, thus giving America the distinction of having the world's largest leper colony. A laboratory for the study of leprosy has been established, in which every effort is made to find and use remedies believed to be efficacious in the treatment of the disease. Considerable success has been had through the administration, by the hypodermic method, of a chaulmoogra-oil mixture. A number of apparent cures have taken place. Most of the Oriental countries are now giving this treatment a trial and cures have already been reported from many of them.

In Manila, a modern water system has been constructed at a cost of approximately two million dollars. The water is obtained from an uninhabited watershed, an improvement which has resulted in a reduction of approximately 800 deaths annually. Water has also been made available in many sections of the city not previously supplied. At a cost of another two million dollars, a modern sewer system was installed.

Hundreds of artesian wells have been bored in different parts of the islands. In many sections in which artesian-well water is exclusively used, the death rate has fallen one half.

Beriberi, which in former days caused frightful mortality in jails and public institutions, has been brought under control through a governmental order which prohibits the use of polished rice in public institutions. This fact is gradually coming to the attention of the masses, and there is reason to hope that in the future the number of deaths from beriberi among the general population will be considerably reduced.

Modern sanitary market buildings constructed of reinforced concrete have been built all over the archipelago. These have been a great factor in the cleanly and economical distribution of food and at the same time an important source of municipal revenue.

It is the frequent comment of travelers that Manila is one of the cleanest cities of the world. The streets are swept daily. Garbage is collected every night. Largely as a result of these two measures, Manila is almost a flyless city. Plague has been eradicated. By making available safe water and by active educational propaganda, the spread of amebic dysentery has been checked. Laws are now enforced for the proper laying-out of cemeteries, and for proper burials. Streets and alleys have been cut through the congested districts of the city. Many thousands of residents have been removed from low swampy lands to higher sites. Modern, dangerous-communicable-disease hospitals have been built in Manila and elsewhere, and the people, educated to an appreciation of such institutions, now willingly avail themselves of their use. The government has built a hospital for the insane, where at least the more violent cases and those urgently in need of care can receive attention. A large general hospital, with a capacity of 350 beds, has been built in Manila. It is one of the most modern in the Orient. A nurses' training school, with over 300 young Filipino students, men and women, is in successful operation; its graduates are already rendering most important service. A medical school, with modern laboratories and the latest equipment for teaching by whole-time instructors who are specialists in their respective branches, was organ-

ized in 1906. It has a five-year course and its graduates are assuming positions of medical responsibility. An anti-tuberculosis society has been formed, and an active educational propaganda is in progress. A hospital has been established at Baguio for incipient cases of tuberculosis, and sanatoria are being conducted in Manila and other places.

Manila now has the most complete set of sanitary ordinances of any city in the world, and in many directions greater sanitary progress has been made than elsewhere. No doubt many of the countries in the Orient feel themselves compelled to join the movement for modern sanitation instituted in the Philippines. They well understand that the crystallized opinion of the world demands more and more that conditions in other Oriental countries must be made to compare with those of higher standard. Before the lepers of the Philippines were segregated, scarcely any Eastern country had segregated lepers. The maritime quarantine practices of the Philippines are being emulated, and agreements are being entered into between the different countries for the control of dangerous communicable diseases.

Largely through the efforts of the medical men of the Philippines, the Far Eastern Association of Tropical Medicine was organized. This bringing together of the medical profession of the various countries has resulted in the promotion of good will and the interchange of ideas, all of which has been mutually beneficial. Instead of viewing the medical men of the Philippines with suspicion, their brethren of other countries now meet with them in full fraternity. The influence that this has had in promoting better understanding and progress can scarcely be estimated. Previous to America's advent in the Orient, fraternizing among the officials in the different countries was scarcely known. Each remained in his own little sphere and much labor and effort were wasted in solving problems which had already been successfully met in other lands. Now there is free interchange of ideas and the knowledge gained in one country is available in a very short time in others.

The death rate in Manila was reduced from 46.83 in 1904 to 23.18 in 1914. This means a saving of over 5,000 lives per annum.

The total reduction throughout the islands is more than 60,000 lives a year. The death rate among the civil employees steadily declined and in 1915 was 3.88 per thousand per annum. It is small wonder that results such as these, achieved entirely under civil regime and with the limited revenues of the islands, should commend themselves to other countries, and it is a fact that the achievement of American sanitation in the tropics has produced a profound impression. When the Rockefeller Foundation, through its International Health Board, entered the field, it found the world in a receptive mood toward American methods.

The conception that the establishment of public-health agencies can be stimulated through hookworm control has won rapid acceptance and has already a good record of achievement. It is realized that if public-health measures are to be successful they must be brought about upon the demand of the people rather than be imposed upon them. To gain this end much effort has been expended in bringing home to the people of tropical countries the practicability of curing hookworm disease.

This disease is one of the few over which the medical profession exercises complete control: first, its cause is definitely known; second, a person afflicted with it can be cured with certainty; third, its prevention is completely practicable. Furthermore, when measures to prevent soil pollution are carried out, other intestinal affections such as typhoid, cholera, and dysentery, largely disappear. Thus, the improvement made in public health more than justifies the money spent in hookworm control.

Even more important is the interest awakened in the people. The work in connection with the relief and control of hookworm infection comes very close to the home life. It causes the speedy substitution of rosy cheeks for pale anemic faces, a result that can be understood by the most ignorant of the community. Moreover, credulity is not strained by being asked to believe in bacteria which can not be seen and which too often are regarded as mythical. The worms which are expelled are plainly visible to the naked eye. Hookworm measures, then, are capable of creating a genuine interest in public health in the masses, who, quickened to a reali-

zation of the possibilities from control measures, soon demand relief from other preventable diseases. Health officers are sought and their work is welcomed instead of being regarded as an intrusion upon personal liberty. The interest which was awakened by the achievements of the American sanitarian is being followed up by the International Health Board through coöperation with the governments of many countries. In the East alone, coöperative measures have been carried out in Egypt, India, Ceylon, Straits Settlements, Seychelles, Fiji, Papua, Siam, Java, Australia, and negotiations are in progress for the further extension of the work. Thus the United States, a nation that was almost entirely ignorant of tropical sanitation when it entered upon its war of 1898, is now gradually assuming a position of importance in this remarkable field. The establishment of educational institutions has followed hand in hand with the sanitary work, so that in the future the natives of the Philippines may have the knowledge to achieve health results for themselves.

An important outcome of America's entrance into the field of tropical sanitation is the reflex stimulus which has been produced in the United States. We are emulating in our own country the wonderful achievements which we ourselves have helped to accomplish in the tropics. But the greatest effect has been to the world at large. The impetus which sanitation in the Orient has received during the past few years has contributed greatly to the well-being of mankind, and America's efforts, which have been made largely through altruistic motives, have added no small share.

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No. 2.

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A CRITICAL SURVEY OF THE SENSE OF HEARING IN FISHES.

By G. H. PARKER.

It was the opinion of many ancient writers that fishes could hear. Thus Aristotle in his "History of Animals," Book IV., Chapter 8, after having stated that fishes possess no evident organs of hearing, declared that nevertheless they must hear, for they flee from loud noises such as those made by the oars of a trireme. Aristotle added further that fishermen were careful to avoid making a noise with their oars or their nets when they perceived many fishes collected together, and he concluded that it was evident from these considerations that fishes have a sense of hearing.

Among the Latins Pliny in his "Natural History," Book X., Chapter 89, stated that though fishes were without ears, yet it was quite certain that they could hear, for it was a well-known fact that in some fish-ponds, the fishes were called to their food by the clapping of hands and that in the fish-ponds of the Emperor they came each kind in response to its name. Thus, notwithstanding that these older writers sometimes confused dolphins and other cetaceans with true fishes, they had from unquestionable sources abundant evidence upon which to base their opinions.

The credit of having discovered, contrary to the belief of such authorities as Aristotle and Pliny, that fishes really possess internal ears, seems to rest with Casserius (1610). This discovery was quite in keeping with the opinion of the times as may be inferred from the conversation between Venator and Piscator in that delightful repository of ancient fish lore, "The Complete Angler." In the first edition of this classic (1653, p. 128) Walton makes Venator put the question to him "But Master, do not Trouts see us in the night?" And to this query Walton, in the guise of Piscator, replies, "Yes, and hear, and smel too, both then and in the day time." Whereupon he adds an account of an experiment by Sir Francis

Bacon to show that sound is easily conducted through water and he concludes with the statement that this experiment "has made me crave pardon of one that I laught at, for affirming that he knew Carps come to a certain place in a Pond to be fed at the ringing of a Bel; and it shall be a rule for me to make as little noise as I can when I am a fishing, until Sir Francis Bacon be confuted, which I shall give any man leave to do." In the second edition of "The Complete Angler" (1655, p. 175) Piscator, who seems to have pondered the matter of fish hearing in the two years since the first edition appeared, added the following final touch. "All the further use that I shall make of this, shall be to advise Anglers to be patient, and forbear swearing, lest they be heard, and catch no fish."

In the eighteenth century the ears of fishes were studied by such workers as Klein (1740), Geoffroy (1780), Hunter (1782), Monro (1785) and others. Hunter (1782, p. 383), in commenting on the function of the ears of fishes, makes the following statement:

Thus Hunter confirmed the opinion of previous investigators, who were further supported by what was learned of the structure of the fish ear by a host of later workers including such men as Comparetti (1789), Cuvier (1805), E. H. Weber (1820) and especially G. Retzius (1881), whose monumental work on the ears of vertebrates may be said to have completed a chapter in our knowledge of this sense organ.

Retzius (1881) has reported very fully on the structure of the

"As it is evident that fish possess the organ of hearing, it becomes unnecessary to make or relate any experiment made with live fish which only tends to prove this fact; but I will mention one experiment, to shew that sounds affect them much, and is one of their guards, as it is in other animals. In the year 1762, when I was in Portugal, I observed in a nobleman's garden, near Lisbon, a small fish-pond, full of different kinds of fish. Its bottom was level with the ground, and was made by forming a bank all round. There was a shrubbery close to it. Whilst I was laying on the bank, observing the fish swimming about, I desired a gentleman, who was with me, to take a loaded gun, and go behind the shrubs and fire it. The reason for going behind the shrubs was, that there might not be the least reflection of light. The instant the report was made, the fish appeared to be all of one mind, for they vanished instantaneously into the mud at the bottom, raising as it were a cloud of mud. In about five minutes after they began to appear, till the whole came forth again."

ears of no fewer than forty-eight species of fishes. The completely differentiated internal ear of one of the higher fishes consists of a utriculus (Fig. 1, *u*) with its three semicircular canals and a sacculus (*sc*) with its appended lagena (*lg*). The utriculus is ordinarily

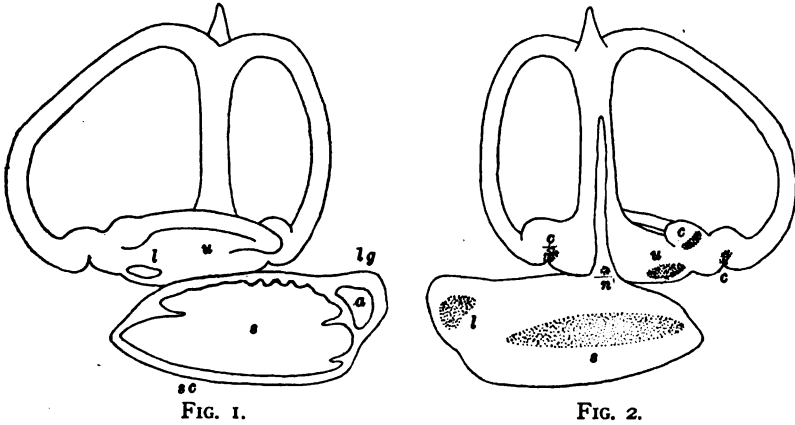


FIG. 1.

FIG. 2.

FIG. 1. Left Ear of the European Perch, *Perca fluviatilis*, lateral view, showing the three otoliths; *a*, asteriscus; *l*, lapillus; *lg*, lagena; *s*, sagitta; *sc*, sacculus; *u*, utriculus. After Retzius.

FIG. 2. Left Ear of the European Perch, *Perca fluviatilis*, median view, showing the sensory patches; *c*, crista acustica; *l*, lapilla acustica lagenæ; *n*, macula acustica neglecta; *s*, macula acustica sacculi; *u*, macula acustica utriculi. After Retzius.

connected with the sacculus by the utriculo-saccular canal. The sense organs in this type of ear reach a maximum number of seven: a crista acustica in the ampulla of each of the three semicircular canals (Fig. 2, *c*), a macula acustica (*u*) in the utriculus and a second one (*s*) in the sacculus, a macula acustica neglecta (*n*) in the utriculus, and a papilla acustica (*l*) in the lagena. No fish is known to possess a papilla acustica basilaris cochleæ or organ of Corti, which makes its first appearance in certain amphibians and is found in all higher vertebrates. Three otoliths are commonly present in the ears of the higher fishes: a large one, the sagitta (Fig. 1, *s*), on the macula acustica in the sacculus, a smaller one, the asteriscus (*a*), in the lagena, and a still smaller one, the lapillus (*l*), on the macula acustica in the utriculus.

Some fishes show considerable divergence from the plan of structure just laid down. Aside from amphioxus, which possesses no ears at all, the cyclostomes exhibit the simplest and probably the most primitive type of this sense organ. In these fishes each ear consists of a single sac with never more than two semicircular canals corresponding very probably to the anterior and the posterior vertical canals of the higher vertebrates. There are three sense organs, a crista acustica for each of the two canals and a macula acustica communis on the wall of the sac. In all higher fishes each ear-sac is double, as already described, consisting of a sacculus and a utriculus with its three semicircular canals. This type of ear possesses ordinarily the seven sense organs already enumerated, the macula acustica neglecta being, however, occasionally absent. In the elasmobranchs the utriculus and sacculus of a given ear communicate freely with each other through a relatively large opening. In the teleosts and other higher fishes a narrow tube, the utriculo-sacculus canal, may connect these two parts, or they may be quite disconnected and separate. Of the thirty-three species of teleosts reported on by Retzius, eleven possessed a well-developed utriculo-sacculus canal, two showed traces of it, and twenty were without the least sign of it, though in embryonic stages they presumably possessed it. These are the chief facts in the comparative anatomy of the ears of fishes. As the terminology shows, these organs were regarded as organs of hearing and this opinion was the prevailing one among scholars of the last century. It has been more or less tacitly assumed in the more important text-books of that period such as Owen (1866), Wiedersheim (1883), Gegenbaur (1898), and others.

The first noteworthy opposition to this opinion came from de Cyon (1878). This investigator, in his study of the function of the semicircular canals in vertebrates, made the observation (p. 93) that lampreys did not respond to sounds and that after their internal ears had been removed, in itself a relatively simple operation, they exhibited great disturbances in locomotion. These disturbances were to be observed seven weeks after the operation and were presumably permanent. De Cyon, therefore, concluded that the ears in this primitive fish were concerned with responses to spacial relations and had nothing to do with hearing. This opinion was supported

by the fact that the ear of this fish was unprovided with a cochlea, that organ which is present in the ears of the higher vertebrates and is especially concerned with hearing.

Some seventeen years later and apparently without knowledge of de Cyon's results, Kreidl (1895) undertook the study of the function of the fish ear. His work was carried out on the goldfish (*Carassius auratus*) and with much care and many precautions. Normal fishes in a carefully guarded aquarium were found not to respond to sounds produced in the air, or even in the water itself, though the creatures did react to a blow on the cover of the aquarium. Fishes poisoned slightly with strychnine were more sensitive and, though they did not respond to a bell or whistle sounded in the air nor to a metallic rod made to vibrate in the water, they did respond to the tapping of the rod, to the clapping of hands, and to the report of a pistol. After the removal of the ears, the equilibrium of these fishes was greatly disturbed, as was to be expected from the previous work of Loeb (1891a, 1891b), Lee (1892, 1893, 1894) Kreidl (1892), and Bethe (1894, 1899), but the animals showed no change in their responses to sounds. Kreidl (1895, p. 464), therefore, concluded that it could not be shown that the goldfish hears and that the responses that this fish exhibits to sound-waves were dependent upon a specially developed skin-sense.

The year following, Kreidl (1896) carried out some simple but conclusive experiments at Krems where large numbers of trout and other fish were bred for market purposes and where the fish were said to come for food at the sound of a bell. Kreidl showed that when the bell was rung by an unseen person, the fishes failed to assemble and that the real stimuli that caused them to come together was the sight of the keeper and the vibration of his tread. Thus Kreidl was confirmed in his view that fishes, including both goldfishes and trout, do not hear.

Kreidl's papers were soon followed by one from Lee (1898), who tested a number of species of fishes by subjecting them to the sounds of the human voice, the clapping of hands, and the striking of stones both above and under water. Though the fishes tested proved to be very sensitive to the jarring of the tank in which they were and to concussions on its walls, they did not respond to sounds produced

as already described and Leë (1898, p. 138) concluded that fishes do not possess the power of hearing, in the sense in which that term is ordinarily used, and that the sole function of their ears is equilibrium.

These conclusions were not supported by the work of Parker (1903a, 1903b) on *Fundulus heteroclitus*. Recognizing the possibility that sound might stimulate not only the skin and the ear but also the organs of the lateral-line system, three sets of *Fundulus* were tested. One set was entirely normal. A second set was prepared by cutting the roots of the fifth and seventh nerves, the lateral-line nerves, and the spinal cord a short distance behind the skull, thus rendering inoperative the lateral-line organs and the organs of touch on the whole surface of the fish except in the region immediately about the pectoral fins. In this set the ears were left intact. In the third and last set the eighth nerves were cut, thus eliminating the ears, while the receptivity of the skin was not interfered with.

These three sets of fishes were subjected to sound stimulation in a large aquarium. The sound was generated by plucking a bass-viol string attached to the wooden end of the aquarium and so arranged that its vibrations were transmitted directly through the wood to the water of the aquarium. The normal fishes responded by pectoral-fin movements in 96 per cent. of the trials. The fishes in which the skin had been rendered insensitive, though greatly reduced in their powers of locomotion by the operations they had undergone, nevertheless responded in 94 per cent. of the trials. Finally the fishes in which the ears had been eliminated responded in only 18 per cent. of the trials. It was, therefore, concluded that sounds called forth responses in *Fundulus* by stimulating not only the skin but also the ears, in other words, that this fish hears. To remove any doubt as to the nature of the stimulus, an electrically driven tuning-fork of the rate of 128 complete vibrations per second was made to replace the bass-viol string on the wooden end of the aquarium. When the fork was in vibration, its base could be brought in contact with the wall of the aquarium and withdrawn at will. If this operation was carried out with a motionless fork, no response from the fishes was to be observed, but when the fork was

in vibration normal fishes and fishes in which the skin was insensitive responded quite regularly with fin movements whereas those in which the ears had been eliminated showed no reactions. Hence there seemed to be no doubt that the ear of *Fundulus* was stimulated by tones.

In view of the discrepancy between the results of Kreidl and those of Parker, Bigelow (1904) was led to retest the goldfish. Three sets of fishes were prepared corresponding to those that had been used in *Fundulus* by Parker. These sets were subjected to the tones from an electrically driven tuning-fork led into the water in which the fish was by bringing the base of the fork into contact with the wooden side of the aquarium. Normal fishes responded in 78 per cent. of the trials. Fishes with insensitive skins but normal ears reacted in 80 per cent. of the trials. While fishes in which the eighth nerves had been cut gave no responses whatsoever to the tone of the fork. These results agreed in the main with what had been obtained by Parker in *Fundulus*, but disagreed with Kreidl's results on the goldfish. Bigelow, therefore, sought for the grounds of this disagreement. For this purpose he repeated exactly Kreidl's procedure in preparing the fishes and instead of eliminating the ear by cutting the eighth nerve, he removed this organ by opening the skull and withdrawing the semi-circular canals and the attached parts of the ear as Kreidl had done. On testing such goldfishes, they were found, as Kreidl had asserted, to respond to tones as normal fishes do, but on dissecting them, it was discovered that by this method only the utricle had been taken out with the semicircular canals and that the saccule, uninjured and intact, had been left behind. It was, therefore, clear that Kreidl's operation removed only part of the ear and that the portion left behind was the very part most likely to be concerned with hearing. Thus the discrepancy between Kreidl's work and that of Parker and of Bigelow was cleared away.

Following these results came a series of papers that were in part favorable to the opinion that fishes could hear and in part opposed to this view. Of those in opposition the first was by Körner (1905). This author tested twenty-five kinds of fishes that had become

accustomed to life in aquaria.¹ The source of sound was a "cri-cri," a child's toy consisting of a slightly deformed metal key which on being depressed gave forth a momentary high-pitched, penetrating sound. This sound was made under water at a distance of 30 to 60 centimeters from the fish and was in no instance followed by a response. Körner (1905, p. 126), therefore, concluded that hearing was an unproved function for the ears of fishes.

Marage (1906) was also unable to get any responses from seven species of fishes subjected to synthetic vowel sounds led into the water through a rubber tube closed by a thin rubber diaphragm. Six of these fishes (*Gobio fluviatilis*, *Anguilla vulgaris*, *Esox lucius*, *Tinca vulgaris*, *Cyprinus carpio*, and *Leuciscus rutilus*) were tested in confined water and one (*Alburnus lucidus*) in the open.

Brüning (1906) noted that stickelbacks in an aquarium were not disturbed by the clapping of hands even when this was done close to the top of the water and that fishes in a pond did not respond to a cry though they were startled by the tread of the observer on the bank.

Maier (1909) installed under water in an aquarium an electric bell so wired that it could be controlled from outside. With this device he tested eleven species of marine fishes (*Gadus morrhua*, *Clupea harengus*, *Ammodytes lanceolatus*, *Trigla gunardus*, *Cottus scorpius*, *Rhombus maximus*, *Solea vulgaris*, *Pleuronectes platessa*, *P. flesus*, *P. limanda*, and *Raja clavata*) and twelve species of fresh-water fishes (*Cyprinus carpio*, *Alburnus lucidus*, *A. bipunctatus*, *Idus melanotus*, *Gobio fluviatilis*, *Barbus fluviatilis*, *Rhodeus amarus*, *Anguilla vulgaris*, *Macropodus* sp., *Anabas* sp., *Osphromenus* sp., and *Girardinus* sp.). To the sound of the bell no reaction of any kind was given by any of these fishes and Maier (1909, p. 394) concluded that they possessed no powers of hearing. Nevertheless he was surprised to find in connection with another line of experi-

¹ The fishes tested by Körner (1905, p. 123) were as follows: *Abramis blicca*, *Cobitis fossilis*, *Gasterosteus pungitius*, *Idus melanotus*, *Petromyzon fluviatilis*, *Rhodeus amarus*, *Betta pugnax*, *Callichthys fasciatus*, *Carassius auratus*, and two varieties, *Chromis multicolor*, *C. tristramus*, *Eleotris* sp., *Gambusia affinis*, *Geophagus brasiliensis*, *Girardinus candimaculatus*, *Haplochilus panchax*, *Heros fasciatus*, *Pacilia mexicana*, *Polyacanthus viridi-auratus*, *Saccobranchius fossilis*, *Tetragonopterus* sp., *Trichogaster fasciatus*, and *T. lalius*.

mentation that the American catfish, *Amiurus nebulosus*, regularly took fright when he whistled. On testing this fish further Maier was completely convinced that it responded to sounds. It was, however, the only fish of those examined by him that so responded.

Bernoulli (1910) tested fresh-water fishes in their natural surroundings with the sounds given out by a submerged electric bell and with shrill whistling. Three species (*Salmo fario*, *Anguilla vulgaris*, and *Lucioperca sandra*) were subjected to the sound from the bell and two (*Salmo fario* and *Thymallus vulgaris*) to whistling. In no instance was there a response.

Haempel (1911) also used the sound from a submerged electric bell and a shrill whistle as stimuli for fishes. Five species of fresh-water fishes were tested (*Cyprinus carpio*, *Scardinius erythrophthalmus*, *Gobio fluviatilis*, *Trutta fario*, and the Zwergwelse = *Amiurus*). None of these fishes reacted to the sounds used except *Amiurus* which regularly responded to both the sound of the bell and to whistling. On removing the ears from a specimen of *Amiurus* and allowing the wounds to heal, the animal lost all response to the sounds employed. Haempel (1911, p. 325), therefore, concluded that while members of the Salmonidæ and Cyprinidæ cannot be said to hear, the Siluridæ and particularly *Amiurus* must be admitted to possess powers of hearing.

In consequence of the results of Maier (1909) and of Haempel (1911) Körner (1916) was led to investigate hearing in *Amiurus*. This fish was subjected to various kinds of shrill whistling, including that from an automobile whistle, to a series of musical tones, to the notes of a scale sung by the human voice, and to the sounds from a "cri-cri." To none of these stimuli was there the slightest response. Körner (1916, p. 263) was unable to explain his negative results with *Amiurus* as compared with the positive outcome of the tests made on the same fish by Maier (1909) and by Haempel (1911).

The papers that have thus far been summarized support in general the conclusion that most fishes do not hear. Those that follow have yielded evidence of an opposite kind. Piper (1906a, 1906b) prepared the ear and the eighth nerve of the pike and of

the eel so that he could demonstrate a demarcation current on these parts. On producing sounds in the water in which the preparations were, an action current was identifiable that lasted as long as the sound did. Such a current was also produced by tapping the walls of the containing vessel, but it did not result from a noiseless jarring of the preparation, nor from a stirring of the water around the preparation. From these results Piper (1906a, p. 296) concluded that fishes responded to sounds by means of their ears.

Parker (1909, 1911a) attempted to ascertain if there was any evidence for hearing in the dogfish, *Mustelus canis*, which, as previous study (1903a, p. 62) had shown, was not responsive to ordinary sound vibrations in water. It was found, however, that if the wooden wall of a tank containing a dogfish was struck by a heavy swinging pendulum, the dogfish within would respond by a sudden jump forward or at least by a waving of the posterior edges of the pectoral fins. The pendulum consisted of a bob weighing 3,800 grams and a suspending wire, the whole apparatus having a length of 260 centimeters. This device was calibrated so as to strike the wall of the tank with a momentum of 83,600 centimeter-gram-second units or more. The minimum stroke was taken as unity and strokes of greater magnitude could be conveniently delivered up to about five times that of the assumed unit. Normal fishes when swimming freely in the water occasionally responded by pectoral-fin movement to a stroke of magnitude 1 and invariably to a stroke of 1.5. After their eighth nerves had been cut, they did not respond to a stroke of less than 3 and invariably only to one of 4. To ascertain if this reduction in sensitivity was due to the operation they had suffered, a second set, in which for other purposes the optic nerves had been cut, were tested with the pendulum. These fishes responded regularly to a stroke of magnitude 2. To eliminate the skin and lateral-line organs, the fifth, seventh, and lateral-line nerves were cut, the spinal cord destroyed up to the neck region and the skin around the pectoral fin cocaineized. Notwithstanding the extent of their preparations, these fishes responded by movements of the pectoral fins to strokes of the pendulum of magnitude 1 to 1.5. Without question their ears were receptive for these vibrations. Parker, therefore,

concluded that though dogfishes are not responsive to ordinary musical tones, they do possess hearing.

Tests carried out by Parker (1910a) on *Ammocetes* by the same means as those used with the dogfish yielded similar results. This fish is sensitive to sound not only through the skin but also through the ears.

Parker (1910b) also studied the ears of *Cynoscion*. In this fish, as in many other acanthopterygians, the sacculus and the utricle are entirely separate structures, there being no utriculo-sacculus canal. *Cynoscion*, after having been in a large wooden tank for some time, became adjusted to its new environment and when the side of the tank was tapped vigorously, it responded by a slight forward spring. The utricle and semicircular canals were then destroyed through a small incision on the top of the head, leaving the sacculus intact. Such fishes showed at once disturbed equilibrium, after which they recovered their upright position. On having blinders put over their eyes, however, they swam with great irregularity. Thus both eye and ear are involved in their responses for equilibrium. During all these tests, however, they reacted as normal fishes do to taps on the wall of the tank, showing that the destruction of the utricle and semicircular canals had not interfered with their responses to sounds. It was found impossible to reverse the operation just described and destroy the sacculus leaving the utricle intact. But by forcing a strong pin through the paper-thin bone between the roof of the mouth and the sacculus, it was possible to fix the large otolith of the sacculus, the sagitta, firmly against the outer or non-nervous wall of the sacculus and thus prevent its independent motion. Fishes treated in this way were only occasionally responsive to taps on the wooden wall of the tank. If a normal fish and one with the sagittæ pinned down were tested in the same tank, the greater responsiveness of the normal individual was easily noticed. Although the experiments on *Cynoscion* leave open the question of the extent to which the skin may participate in sound reception, they show very clearly that the sacculus of the ear, as contrasted with the utricle, has a well-defined part in this activity.

Meyer (1910), whose work was chiefly concerned with the capac-

ity of fishes to associate, showed that goldfishes could be taught to go for food to one or another part of an aquarium depending on the sounding of a high- or a low-pitched bell, a result favorable rather than otherwise to the opinion that goldfish hear.

Without knowledge of the work of Haempel (1911) and of Körner (1916) Parker and Van Heusen (1917) undertook the study of the responses of *Amiurus* to sound and other mechanical stimuli. They were influenced in this by the hardness of *Amiurus* and by the observation of Maier (1909) that this fish responded to a whistle. As in Parker's former experiments, attempts were made to eliminate the ears, the lateral-line organs, and the skin. In two of these operations new methods were devised. In excluding the ear nothing better was found than cutting the eighth nerve. After the operation the necessary incisions on the head quickly healed and the fishes lived well. Following the tests, fishes that had been thus operated upon were dissected to ascertain that the eighth nerves had actually been cut, an almost invariable result. In the elimination of the lateral-line organs those of the trunk were rendered inoperative by cutting the lateral-line nerves near the gill clefts and those of the head by destroying individually the forty-eight organs of that region. This was done by means of an electric depilating needle. Histological examinations of the spots thus treated showed in the preliminary tests the complete destruction of these organs. Finally, the skin was rendered non-receptive by painting it with a 20 per cent. solution of magnesium sulphate, which was allowed to act for five minutes. The skin of a fish so treated remained insensitive to mechanical stimulation for an hour to an hour and a half.

In preparing fishes for experimental tests they were always previously blindfolded by having a pair of thin leather goggle-shaped shields placed over the eyes and held there by a few stitches taken in the skin. Because of its gregarious habits *Amiurus* was always tested in pairs, single fishes being much less satisfactory for experimental work than two. In accordance with the states of their sense organs eight groups of fishes were used: first, normal fishes with skin, lateral-line organs, and ears intact; second, fishes with skin and ears intact but lateral-line organs eliminated; third,

fishes with skin and lateral-line organs intact but ears eliminated; fourth, fishes with only skin intact; fifth, fishes with only lateral-line organs and ears intact; sixth, fishes with only ears intact; seventh, fishes with only lateral-line organs intact; and eighth and last, fishes with none of the three sets of sense organs intact.

The fishes were tested in an aquarium of glass and stone, measuring 75 cm. by 35 cm. by 40 cm. This was supported on an inflated bicycle tire that rested on a table each leg of which pressed on a mass of excelsior wood chippings spread on a tile which in turn had under it a pad of rubber 1.8 cm. thick. The whole apparatus was set up on the concrete floor of a basement room in the laboratory and proved to be remarkably free from extraneous vibrations.

Of the several kinds of sounds to which the fishes were subjected, that from a watchman's whistle² blown vigorously in the air gave most striking results. Of the four classes of fishes in which the ears were intact all responded with clearness and certainty by swimming at once from the upper surface of the water into deeper positions in the aquarium. Those in which the eighth nerve had been cut did not respond at all to the whistle, though they responded to other stimuli, such as currents of water, water dropped on the surface of that in the aquarium, and pendulum strokes on the wall of the aquarium. Incidentally it may be mentioned that the currents of water and the drops of water proved to be stimuli for the skin only, but that the strokes of the pendulum affected not only the skin but also the ear (compare Table I., Parker and Van Heusen, 1917, p. 472).

Another means of stimulating *Amiurus* consisted in a series of tones from a telephone submerged in the water of the aquarium. This telephone was enveloped in a tightly stretched thin rubber bag. By means of a piece of apparatus consisting of a series of seven alternating-current generators with their armatures on a common shaft driven by a ten-horse-power electric motor, currents of 43, 86, 172, 344, 688, 1,376, and 2,752 cycles per second were produced. By appropriate switches any one of these could be thrown into the

² The sound produced by this whistle consisted of at least two elements: a low vibration probably due to the rapid oscillation of the small ball contained in the whistle, and a shrill piping note.

telephone which then yielded a tone of corresponding pitch. These tones were of a musical quality and were accompanied by harmonics. Thus the fishes in the aquarium could be subjected to any one of the seven tones from 43 to 2,752 vibrations per second without the least mechanical jar or disturbance. To be perfectly sure that the operation of the telephone had no effect upon the fishes, except through the sound it produced, its vibrating plate was removed, after which it was operated in the aquarium as in the ordinary tests. Under these circumstances no responses of any kind were obtained from the fishes. The electromagnetic field and such other incidental disturbances necessarily introduced by the telephone were thus shown to be ineffective as stimuli.

The reactions of *Amiurus* to the tones from the telephone are given in the following table:

TABLE I.
RESPONSES OF *Amiurus* TO TONES AT OCTAVE INTERVALS FROM 43 TO 2,752
COMPLETE VIBRATIONS PER SECOND.

Each number represents the number of responses in ten trials, five on each of two fishes.

Conditions of the Fishes.	Pitch of Tones in Complete Vibrations per Second.						
	43.	86.	172.	344.	688.	1,376.	2,752.
1. Normal: skin, lateral-line organs and ears functional..	10	9	7	6	4	0	0
2. Ears functional; skin and lateral-line organs eliminated	10	8	7	4	1	0	0
3. Skin functional; ears and lateral-line organs eliminated	6	4	3	0	0	0	0
4. Skin, lateral-line organs and ears eliminated.	0	0	0	0	0	0	0

From the observations recorded in this table Parker and Van Heusen (1917, p. 477) concluded that *Amiurus* is more generally stimulated by tones of low pitch than by those higher in the scale, that both the ears and the skin are effective as receptors for these tones, but that the ears have a wider range than the skin. These results completely confirm Haempel's conclusion that *Amiurus* can hear.

The judgments that from time to time have been passed in these two lines of evidence have been almost as diverse as the evidence

itself seems to be and much has naturally depended upon the momentary phase of the subject. Lang (1903), after an extended account of the relations of the otocysts of invertebrates and the ears of vertebrates to equilibrium, concluded on the basis of Kreidl's experiments that there is no great likelihood that fishes hear, but that experiments should be tried on fishes that have differentiated structures for the production of sounds. Blochmann (1903, p. XCVI.) on similar grounds also doubted if fishes could hear. Hensen (1904) reviewed the work of Zenneck (1903) and of Parker (1903a) and concluded from their results that fishes do hear, a conclusion that was justly criticized by Bezold (1904, p. 159), who pointed out that Zenneck's results might be explained on the assumption that the skin was stimulated. Somewhat later Zacharias (1906) in a popular article concluded on the basis of the work of Kreidl and of Körner that fishes could not hear and misstated (1906, p. 373) entirely the results of Zenneck and of Bigelow which he claimed supported this conclusion. Two years later Körner (1908) declared that conclusive experimental evidence to show that fishes hear had not yet been produced, but he felt that it was not impossible that they possessed a certain degree of audition. In the same year Edinger (1908) pointed out the relation of sensory reactions to central nervous structures and stated on the basis of Piper's work that with fishes it was rather a question of what did they hear than did they hear. Willem (1913, p. 1247), on the basis of the evidence already cited, argued in favor of hearing. Watson (1914, p. 393), after reviewing the more important statements pro and con on the question of fish hearing, summed the matter up in the sentence: "It seems very difficult to reach any conclusion in the face of such contradictory evidence."

In attempting to sift what has been thus far advanced on the problem of fish hearing, it is natural to begin with the query of what would constitute hearing in a fish. Both Kreidl (1895) and Lee (1898) have discussed this question in the light of their own experiments. Kreidl (1895, p. 461) has pointed out that it is not in accord with ordinary usage to speak of hearing as any sensory disturbance produced in an animal by a vibration propagated through

the surrounding medium. Such disturbances, as has long been known, may stimulate the organs of touch as well as the ear. Kreidl, therefore, rightly maintained that these disturbances must be shown to stimulate the ear before they can be said to be stimuli for hearing. Lee (1898, p. 138) has also emphasized the importance of regarding hearing "in the sense in which the term is ordinarily used." It seems, therefore, fair to conclude that any disturbance that can be said to produce hearing through the human ear may also be said to call forth hearing in a fish provided it can be shown to act through the ear and not simply through the skin or other such receptive surface.

The human ear is normally stimulated by a great variety of sounds, some in the nature of tones and others in the nature of noises. We hear not only the tones of a tuning-fork, but the less pure tones of musical instruments, and of the voice as well as an immense array of very irregular disturbances, difficult to describe from a physical standpoint and classed generally as noises. Perhaps among the most extreme of these are explosive noises such as are produced by the clapping of hands, the discharge of firearms and so forth. All of these we certainly hear, for they affect us chiefly through the ear and their inefficiency as stimuli for the deaf is well known.

When they are extreme, they produce what we commonly speak of as shock or concussion and there has been a tendency on the part of some workers (Bateson, 1890, p. 252) to regard the shock as distinct from the sound. From a physical standpoint there seems to be no grounds for this assured distinction. The powerful disturbance that emanates from the midst of an explosion is not made up of sound and shock or concussion, but is a single complex disturbance which when it strikes our bodies may stimulate ears, skin, and even other sense organs. In so far as it affects our ears, however, we must admit it as a stimulus for hearing. Kreidl (1895, p. 459) has pointed out that sounds with shock quality are more effective as stimuli for fishes than ordinary tones are, and the experimental work of later investigators goes far to substantiate this conclusion. Nevertheless, for reasons already given, this state of

affairs does not militate against the use of this class of sounds as stimuli for the ear. It is, therefore, entirely appropriate to use such sounds in testing hearing in fishes, but the experimenter must show beyond a doubt that they do stimulate the ear, otherwise evidence derived from such tests fails to touch the problem. The test for hearing in fishes is the proved presence of a response mediated by the ear and dependent upon some vibratory physical disturbance in the water which disturbance may vary from the extreme regularity of a pure tone to the extreme irregularity of a noise such as the report of a gun or other like explosion.

In discussing hearing in fishes, Lang (1903, pp. 44, 48) expressed the opinion that these animals probably possess through the ear a sense of trembling (*Erschütterung*, *Erzitterung*) rather than one of true hearing and that this sense of trembling is a forerunner of hearing. In distinguishing the sense of trembling from that of hearing he states that in the former the pressure waves are perceived as a series of more or less distinct and separate entities, whereas in hearing the impression is more homogeneous. This distinction is one that pertains to sensation and, therefore, it can hardly be made the basis of experimental tests in fishes. It, moreover, implies that we cannot be said to hear sound vibrations whose note is so low that the single beats fail to fuse. But that we hear these beats as well as we do tones is beyond dispute and Lang's distinction, therefore, is in reality without support. Something of the same view has been expressed by Bernoulli (1910, p. 639) who, however, assumes the receptor for such beats to be the skin not the ear.

Lang (1903, p. 48) and a few other workers have also intimated that hearing is a process that probably cannot be carried out in water, but is necessarily associated in some way with the air. A little thought, however, will show that this position is quite untenable, for watery fluids bathe the end organs of the internal ears of all vertebrates whether they be inhabitants of the air or of the water. If fishes hear, sounds normally reach their ears much more simply and directly than in the case of air-inhabiting forms, for such disturbances pass at once through fishes' bodies and require no

translation from an air medium to a water medium as they do in air-inhabiting vertebrates. When, therefore, as occasionally happens, a fish takes up with a temporary residence in the air, it should not be expected to be very responsive in this situation to sounds. This seems to be the case with *Periophthalmus phya*, which often deserts the water for the shore and which, when in the air, is apparently quite deaf even to the report of a shotgun (Johnstone, 1903, p. 300). It is only after the development of some form of translating apparatus, such as an ear-drum and a middle ear, that it would be fair to expect such animals to show much response to sounds in the air. Organs of this kind characterize the ears of air-inhabiting vertebrates and represent a means of overcoming an auditory obstacle which fishes have not had to meet, for, as has just been made clear, there is not the least ground for assuming that from a physical standpoint water-inhabiting animals find any impediment to hearing.

It is a well-known fact that sounds produced in the air penetrate water to only a very slight degree and, conversely, that sounds generated in the water pass out into the air only to a correspondingly limited extent. The ordinary surface between air and water is an excellent reflector of sound. Parker (1911*b*, p. 4) found that even the loud noise from a motor boat was only faintly heard by an observer who dove close to the boat and Watson (1914, p. 393), when under four feet of water, was unable to hear the report of a revolver discharged in the air overhead. It is, therefore, not surprising that *Fundulus*, though very sensitive to sounds, did not respond to the report of a saluting charge of two pounds of gun-powder exploded from a six-pound howitzer until the fish was within thirty feet of the muzzle of the gun when to the human ear the sound was deafening (Parker, 1911*b*, p. 8). These conditions were fully appreciated by Bateson (1890, p. 251) when he remarked apropos of certain tests on pollack: "As might be expected, none of the fishes were seen to take notice of sounds made in the air." Such sounds, as has already been shown, fail in large part to enter the water, being mostly reflected from its surface back into the air.

It is probably due to this circumstance, rather than that fishes do not hear, that the tests of a number of investigators who used

sounds generated in the air yielded negative results. Kreidl's (1895, p. 458) inability to stimulate goldfishes by bells and whistles may thus be explained as well as Lee's (1898, p. 137) failure to get responses to the human voice, clapping of hands, and striking together of stones. This may also have been the case with the experiments of Marage (1906), notwithstanding the care with which a translating diaphragm was used, and it seems quite certainly to have been true of Bernoulli's observations (1910, p. 643), according to which *Lucioperca* failed to respond to a pistol shot from a boat at the distance of two kilometers. When fishes in water do respond to sounds made in the air, as in the case of *Amiurus* (Maier, 1909; Haempel, 1911; Parker and Van Heusen, 1917), it must be taken as evidence of very unusual sensitiveness. As a rule such responses are not to be expected, for, as already stated, sound in the air enters water to only a very slight degree.

The production of sounds by fishes is not without its bearing on the question of fish hearing. Kreidl (1895, p. 463) appreciated this side of the problem when he argued that "Die Thatsache, dass es auch Fische gibt, die Töne hervorzubringen im Stande sind, welche möglicher Weise den Zweck haben können, als Lockmittel zu dienen, lässt immerhin die Möglichkeit zu, dass bei diesen Species bereits eine geringe Ausbildung des Gehörorganes stattgefunden hat." The importance of testing such species was emphasized by Lang (1903, p. 48). In the seventh volume of the "Cambridge Natural History," Bridge (1904, pp. 355-365), after remarking that "contrary to popular belief sound-producing or vocal organs are by no means uncommon in fishes," gives an extended account of the various means that fishes possess for the production of sounds. In some instances the sounds produced by them are unquestionably accidental accompaniments of other types of activity, but in other cases the sounds are dependent upon such differentiated mechanisms that it is impossible to attribute these emanations to accident. One instance alone will suffice. Of the fishes studied by Parker (1903a, p. 48: 1910b) *Cynoscion* produces a deep drumming sound audible when the fish is in the air to a distance of at least fifty feet. This sound is produced only by the males (Smith, 1905, p. 377) and Tower (1908) has shown that it results from the vibratory action

of a special muscle on the abdominal organs and particularly on the air-bladder. The females not only do not drum, but they do not possess the drumming muscle. This condition of high specialization, which is doubtless connected with the breeding habits of *Cynoscion*, is common to many of the sound-producing fishes and makes it impossible to agree with Körner (1905, p. 103) in dismissing all such cases as of accidental nature. Though it is possible that fishes produce sounds that are in some way serviceable to them but that they themselves do not hear, it is very unlikely that such is the case and the occurrence of instances of unisexual sound production, as in *Cynoscion*, strongly suggests the presence of the sense of hearing rather than the reverse.

It is reasonable to suppose that if fishes hear, they will show some form of response to sounds. If it could be demonstrated that no fish responds to sounds of any kinds, it would be highly improbable that fishes heard. Several investigators have thus tested fishes and, without reference to skin or ear, they have attempted to ascertain whether in fact fishes respond to sounds at all. Such investigations are fundamentally important for the problem at hand but, as already explained, they do not allow of a discrimination between touch and hearing. Bateson (1890, p. 251) noticed that to the vibrations from blasting pouting scattered, sole, plaice, and turbot buried themselves, and congers drew back a few inches. To a blow on the aquarium wall pollack made an obvious response. Kreidl (1896, p. 585) stated that *Salmo iridens* was stimulated by the vibration from the human footfall. Zenneck (1903) found that *Leuciscus rutilus*, *L. dobula*, and *Alburnus lucidus* swam away from an electrically driven bell immersed in a stream. Parker (1903a, p. 62) showed that mackerel (*Scomber scombrus*) and menhaden (*Brevoortia tyrannus*) responded to the vibration of a cord applied to an aquarium. Lafite-Dupont (1907) found that, except for two elasmobranchs (la Roussette, la Torpille), the other fishes tested (le Grondin papillon, la Vieille, le Mulet, la Sole) were responsive to a stroke on the side of the containing vessel. Parker (1912) found that certain fishes, *Tautoga*, *Stenotomus*, *Menticirrhus* and *Sphaeroides*, avoided the end of an aquarium at which blows were delivered by a swinging pendulum, that *Prionotus* gathered near this

source of sound, and that *Fundulus*, though much disturbed by the sound, tended to go neither toward the source nor away from it. These positive results show that many fishes respond to noises or even tones, but they do not throw light on the question of the particular sense organ concerned and consequently it cannot be stated whether they are due to stimulation of the ears or of the integumentary sense organs or of both.

As opposed to this line of evidence several investigators have reported lists of fishes that are said not to respond to sounds in any way. As already noted in an earlier part of this paper, Körner (1905) recorded twenty-five kinds of fishes none of which responded to the sounds from a "cri-cri." This is certainly a formidable list. When Körner learned through the work of Maier (1909, p. 394) and of Haempel (1911, p. 325) that *Amiurus* reacted to a whistle blown in the air as well as to sounds from a submerged electric bell, he undertook to test this fish with a variety of whistles, the human voice, and other sound-producing devices including the "cri-cri." His results were completely negative (Körner, 1916, pp. 263, 267), and he confessed his inability to explain the conflict between this outcome and the results of Maier and of Haempel. Parker and Van Heusen (1917) have shown not only that *Amiurus* is receptive to sounds but that, in respect to this stimulus, it is an exceedingly sensitive fish. Their method of work throws some light on Körner's results. When *Amiurus* was to be tested by them for response to sound, blindfolded individuals were put into a large aquarium. Here they appeared to settle themselves quickly near the bottom and to assume in a short time a condition in which it was reasonable to carry out tests. But in this state they seldom responded to sounds and it was only after they had been some hours, or better a day or so, in the aquarium that they really arrived at a condition of responsiveness. After this period they began to desert the bottom and to swim in the upper water, and in this state they were most responsive to sound. When thus swimming near the top, a blindfolded *Amiurus* would immediately descend to the deeper water in response to a very slight finger-tap on the slate wall of the aquarium. It was only under these conditions that Parker and Van Heusen obtained responses to a whistle or to sounds from the

telephone. If the hand of the experimenter was held in the aquarium water, be it ever so carefully done, the *Amiurus* immediately descended to the deeper parts and responses to the more delicate forms of stimuli were completely inhibited. Hence Körner's method of operating a "cri-cri" by hand under water could have had no other result than that of rendering the fishes quite unresponsive and it would have been surprising if he had obtained anything but negative results. As this responsive phase of *Amiurus* seems to have entirely escaped Körner's attention, it is natural that he should also have failed to observe the reaction of this fish to whistles, and to other sound-producing devices. Hence so far as *Amiurus* is concerned Körner's negative results, as contrasted with those of Maier (1909), of Haempel (1911) and of Parker and Van Heusen (1917), are quite clearly due to defective technique and as this technique was also the basis of his tests of the twenty-five kinds of fishes first reported by him as without hearing, it follows that these tests can no longer be regarded as valid and that Körner's statements based upon them are, therefore, without weight.

Another source of error in the testing of fishes for hearing is the assumption that their only form of response to sound is flight. From the time of Aristotle this has been known to be a typical response, but that it is the only method of reaction to sounds is far from true. Kreidl (1896, p. 585) in his experiments at the fish basins in Krems got evidence that certain fishes would approach a center of vibratory disturbance and Parker (1912, p. 103) showed that *Prionotus*, which produces a loud grunting noise, approaches a sound center rather than retreats from it. Thus, though fishes under most experimental conditions commonly are put to flight by sounds, they occasionally may do the reverse and under more natural conditions this may be a much more usual form of response than has been suspected. But whether fishes approach or avoid a source of sound, their responses in such activities are chiefly through their fins. It is, therefore, not surprising that in experimental tests sound, and particularly slight sounds, call forth very characteristic fin movements. As these movements follow with such regularity on the application of this stimulus, to deny them as a sign of effective stimulation is to ignore that very feature which may be of prime

importance in the determination of an experimental result. Hence it is not surprising that Haempel's outcome on *Cyprinus*, *Scardinius*, *Gobio*, and *Trutta* should have been negative, for he states (1911, p. 320) at the outset that movements of the pectoral fins, of the caudal fin, and of the respiratory apparatus, however called forth, are not accepted by him as evidences of sound stimulation. To any one familiar with the responses of fish such a declaration must seem to say the least, arbitrary and condemns without further ado any negative results that its author might claim. Such movements are often most characteristic and significant and they call for close scrutiny and careful observations. Although they can be seen clearly and beyond question when the fishes are in aquaria, they would very probably escape attention when these creatures are at some distance in open water. In consequence it seems doubtful if negative results recorded under these conditions (Bernoulli, 1910, p. 640) can be said to be well grounded.

From the observations of Parker and Van Heusen (1917, p. 477), it is clear that *Amiurus* is by no means equally responsive to tones of different pitches. It responded with greatest certainty to tones of 43 complete vibrations per second, and with less and less certainty to succeeding octaves up to 688. It failed entirely to respond to the two tones above 688, namely 1,376 and 2,752. It is, therefore, clear that *Amiurus* is much more receptive to tones of a low pitch than to those of a high pitch. Since most of the sounds produced by fishes are of low pitch, being described usually as croaking, grunting, or drumming sounds, it is probable that fishes are adapted chiefly to this class of tones. It is, therefore, not impossible that many tests that have yielded negative results may have done so because the tones employed were too high in pitch for the fishes. This may have been the case in the sound from the "cri-cri" employed by Körner (1905, 1916) and with that from the electric bells used by Maier (1909), by Bernoulli (1910), and by Haempel (1911). If the sounds thus produced were out of range for the fishes, it is not to be expected that they would react. All such tests, therefore, that have yielded negative results are open to this objection until doubt on this point has been removed. Thus the negative evidence of practically all the recent workers on this sub-

ject is thrown under suspicion and it, therefore, remains to discuss this problem from the standpoint of the few cases of positive evidence.

These few instances cover a considerable range of fishes. They begin with *Ammocetes* which is apparently not responsive to ordinary noises (de Cyon, 1878, p. 93) though it will react by a winking movement of its oral hood and by curving its body when the wall of its aquarium is struck by a swinging pendulum. After cutting the eighth nerves, these responses can be called forth only by a stroke at least three times as strong as in the previous instance, thus showing that the ear is decidedly more sensitive to this stimulus than the other receptors in the body, very probably those in the skin (Parker, 1910a, p. 470).

Mustelus exhibits conditions very similar to those in *Ammocetes*. It is not responsive to tones (Parker, 1903a, p. 62) and to ordinary noises (Lafite-Dupont, 1907), but it reacts with a sudden jump forward or a quivering of the pectoral fins to a pendulum stroke on the wall of its aquarium (Parker, 1909, 1911a, p. 48). On cutting the eighth nerves, three times the former stimulus was required to call forth the response previously noted. This fin-movement remained normally elicitable in fishes whose skin had been desensitized by combined nerve-cutting and treatment with cocaine, but disappeared entirely from them on cutting their eighth nerves. Thus *Mustelus* is responsive through the ear, and less so through the skin, to the noise produced by a stroke on the wall of its aquarium.

Among teleosts three cases call for consideration: *Fundulus*, *Carassius* and *Amiurus*. The grounds for concluding that *Fundulus* (Parker, 1903a) and *Carassius* (Bigelow, 1904) hear have already been briefly stated in the earlier part of this paper. Each fish responds by at least fin-movements to the tones of a tuning-fork and to other sounds. These responses cease in part or wholly on cutting the eighth nerves. They are not greatly reduced by very extensive nerve-cutting through which much of the skin can be rendered insensitive. The responsiveness of the fishes under these conditions shows that the operation of cutting the eighth nerve cannot be regarded as the occasion of the decline in sensitivity of the particular group in which this operation was carried out but that this decline

must be ascribed to the loss of the ear as a receptor. Hence the futility of the objection that the cutting of the eighth nerve involves in itself serious inhibition. Watson (1914, p. 394) has urged against these results the criticism that the sound-producing apparatus "used by Parker and by Bigelow," an electrically driven tuning-fork, "is open to the severest kind of criticism." No further comment is made on this point and the reader is left in uncertainty of what should have been used except for the remark (p. 394) that it is strange that Parker did not repeat Bateson's experiment of tapping stones under water. Such comments as these show a very imperfect appreciation of the conditions under which tests on fish hearing can be carried out, for it is extremely doubtful if anything of value could be obtained by Bateson's procedure whereas that so severely condemned yielded position results. Hence there appears to be no good grounds to oppose the conclusion that both *Fundulus* and *Carassius* hear.

Notwithstanding Körner's negative results (1916) the unusual responsiveness of *Amiurus* as shown by Maier (1909), Haempel (1911), and Parker and Van Heusen (1917) is beyond doubt and Haempel's tests of a fish from which the ears had been removed is strongly indicative of hearing. This conclusion is abundantly confirmed by the much more extensive experiments of Parker and Van Heusen already summarized. The fact that these investigators used a submerged telephone as a source of sound and avoided much of the nerve-cutting previously employed in eliminating lateral-line organs and the skin has removed practically all of the assumed objections to the earlier work of Parker. They confirm, beyond doubt, Haempel's conclusion that *Amiurus* can hear.

The part of the fish ear concerned with hearing has not yet been determined with certainty. The condition seen in many of the higher fishes in which the two chief parts of the ear, the utricle and the saccule, are completely separated, suggests at once different functions for these parts. And the fact that in the goldfish the animal still responds to sounds after the removal of the utricle and its appended canals (Bigelow, 1904) offers the natural suggestion that in this fish hearing is associated with the saccule. This view is supported by Parker's observation (1910b) that when the

large otoliths in the sacculi of *Cynoscion* are pinned off against the non-nervous walls of these organs, responses to sounds largely cease, whereas a destruction of the utriculi and semicircular canals does not affect hearing. These observations support Piper's conclusions (1906a, 1906b) based on experiments involving what were without doubt the saccular otoliths. Thus, the sacculus, rather than the utriculus, seems to have to do with hearing in fishes. In this connection it is interesting to record the observations of Smith (1905, p. 378) to the effect that in those sciænid fishes that make drumming noises the otoliths from the sacculi are exceptionally large, whereas in *Menticirrhus*, a sciænid which does not drum, they are relatively small, thus suggesting a relation of the sacculus to hearing as was suspected by Scott (1906, p. 49). Without, therefore, putting too great confidence in these somewhat fragmentary observations, it seems probable that in the ears of the higher fishes where utriculus and sacculus are well differentiated, the sacculus has to do with hearing and the utriculus with equilibrium.

The bearing of this conclusion on the functional interpretation of the parts of the internal ear in the higher vertebrates must be obvious. It points at once to the macula acustica sacculi as a possible organ of hearing. Whether, in mammals, for instance, this saccular organ is concerned with hearing or not must, of course, be settled by experiment (compare Richard, 1916), but so far as the condition in fishes is concerned, it is not unreasonable to anticipate an auditory function for it. Its function, however, must be very different from that of the cochlear organ, for while the cochlea is without much doubt the organ of the ear concerned with tone discrimination, the macula acustica sacculi is probably at best only a means of distinguishing between the presence or absence of sound, including possibly its intensity. In this primitive way fishes probably hear, for it is unlikely, since they lack a cochlear organ, that they respond in any differentiated way to differences of tones. Their hearing is probably to be compared to the vision of the totally color-blind, rather than to that form of vision in which colors are discriminated.

But the fish ear is not only primitive in itself; it exhibits in its various conditions several grades of proficiency. In not a single

primitive fish, cyclostome or elasmobranch, has the ear been shown to be a receptor for what may reasonably be called tones. The ears of these lower fishes are stimulated only by relatively loud noises such as have been shown to be effective stimuli for the skin. In the higher fishes, the teleosts, the ears are not only stimulated by noises of the kind just mentioned, but they are stimulated by much less intense sounds and sounds more in the nature of tones. In this respect they mark a great advance over the condition found in the lower fishes, a condition probably phylogenetically earlier.

From this standpoint it is maintained that fishes from the cyclostomes to the teleosts have been shown to have, in varying degrees, powers of hearing. While it is easy to agree with Haempel (1911, p. 325) that *Amiurus* can hear, it is quite impossible to accept his further conclusion that "unter den Süßwasserfischen einzig und allein den Welsen die Fähigkeit des Hörens zukommt." That these fishes are the only ones that hear is so unnatural a conclusion that it carries with it its own refutation.

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April, 1918.

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THE SYRIAC DIALOGUE "SOCRATES."

A STUDY IN SYRIAN PHILOSOPHY.¹

By WM. ROMAINE NEWBOLD.

(Read April 23, 1914.)

In 1858 Paul de Lagarde published in his "Analecta Syriaca" a short dialogue entitled "Socrates." The only known copy is found in that precious Nitrian codex of the British Museum (Add. 14658) which also contains, besides other philosophical works, the only existing texts of the Bardaisanian "Book of the Laws of the Countries" and "The Oration of Melito before Antoninus Cæsar." Notwithstanding the unusual intrinsic interest of the "Socrates," it has been, so far as I have been able to ascertain, quite ignored since its publication. I have seen no translation of the text nor any discussion of the problems which it presents except a brief and misleading statement by Renan (in Duval, "La Littérature Syriaque," p. 270).² It has not been republished and the original edition is now difficult to obtain.

¹ This paper was read before the American Philosophical Society in April, 1914, but publication was deferred in anticipation of the appearance of Mr. Mitchell's second volume (see note 5) which was promised for September of 1914, but was prevented by the outbreak of the war. As this now seems to have been indefinitely delayed, I have decided to publish my tentative conclusions.

² Soon after this paper was written my friend, Mr. Robert Pierpont Blake, brought to my attention V. Ryssel's paper "Der pseudosokratische Dialog über die Seele," in *Rhein. Mus.*, N. F., Vol. 48, pp. 175-95. Ryssel gives a translation, suggests some emendations and adds a few footnotes but does not attempt a systematic interpretation. He thinks it a translation from the Greek and attributes the translation to Sergius of Ras'ain (d. A.D. 536), who was the translator of other texts in the same volume. Whether the dialogue was originally written in Greek or Syriac is a question upon which I have not formed a definite opinion, but I am inclined to think it was Syriac. The style as a whole is singularly idiomatic and the occurrence of Greek words and constructions is not conclusive evidence to the contrary in a work obviously imitated from Greek models. The atmosphere is purely

In extent it is not very long, occupying only nine pages octavo. In form it professes to be a dialogue between Socrates and an anxious inquirer named Herostrophus or Erostrophus.* But it contains little in the way of dialogue, the greater part of the book being occupied by a discourse in which Socrates answers Herostrophus's questions.

The author's conception of Socrates bears no resemblance to the Socrates of Plato and but little to the Socrates of Xenophon. He is indeed an oriental sage whose utterances are received as oracles by his admiring hearers, and, although he expresses his views with modesty—the only trace of the "irony" of the historical Socrates—he nevertheless feels that their homage is justified. "O young man," he says to Herostrophus in one passage, "not in vain and not for nought have you come to me to hear my words."

The ostensible theme is the nature of the soul, but in the course of the discussion Socrates reveals the outlines of a system of philosophy which is of no little interest to the student, not because of its intrinsic value, but because of the light which it throws into some dark corners of the history of thought. The elements of this system are those same Platonic, Aristotelian and Stoic ideas which long before the beginning of our era had become the common property of the races that shared the Hellenistic culture. The syncretistic systems into which they were wrought by sundry thinkers are known by many names—Alexandrian, Hermetic, Gnostic, Neo-Pythagorean and Neo-Platonist—but all possess many features in common. Some of these the system of the "Socrates" also presents, but its peculiar interest lies in the fact that the familiar elements are combined in novel fashion. I have indeed been able to discover but one other system which is closely akin to it, that of the Syrian philosopher Bardaisan, who was born in Edessa A.D. 154 and died in 222. It has long been known that Bardaisan exerted no little influ-

oriental, the borrowed ideas are treated as no Greek would treat them and the conspicuous absence of the technical terms of philosophy common in Syriac from the fourth century onward suggests an early date of composition. Whatever the original language, I think it probable that the author was a Syrian; certainly not a Greek.

* Ryssel suggests that the name should be read "Aristippus," for which I see no good reason.

ence during his life and that the Christian Church which he founded endured for five or six centuries after his death, but, until recently, little has been known of his ideas. The discovery and publication of Theodore bar-Koni's⁴ account of his system and of some hitherto unknown works of Ephraim's⁵ have thrown a flood of new light upon him and Mr. Mitchell promises that his second volume, which will appear in the course of a few months, will contain still more valuable information. With the aid of this new material one may recognize in the Syriac "Socrates" a work certainly of the school of Bardaisan. Whether it is from his own hand or not is another question.

The accounts of Bardaisan's philosophy which we possess are so inconsistent that it is necessary to determine which are and which are not trustworthy. The most extended are those of Ephraim, Theodore bar-Koni, Moses bar-Cepha, Moses the Syrian, the Fihrist, and Shahrastani. Of these the first two are the oldest, are in substantial agreement and probably are derived from the same document. That of Moses bar-Cepha is akin to Theodore's but contains Manichæan elements not found in him; in the later documents these elements become still more pronounced. I think it quite certain that these later versions represent the teaching of the Bardaisanian Church after it had been for centuries in contact with the closely related system of Mani. It is quite possible that the system known to Ephraim and Theodore had also been more or less contaminated by the same influences, having been exposed to them for more than a hundred years. The "Book of the Laws," which is the oldest authentic Bardaisanian document, unfortunately gives no definite information upon the points of interest. Ephraim and Theodore therefore must be regarded as the only trustworthy authorities.

The "Socrates" represents bodies as composed of four "elements" or "powers"—earth, wind, fire and water. Bardaisan posited five "powers" or "existents," *ihye*, out of which bodies are

⁴ Pognon, "Les Coupes Mandaïtes," 1898; Addai Scher, "Corpus Scriptorum Christianiorum Orientalium," Vols. 65-66, 1912.

⁵ "St. Ephraim's Prose Refutations of Marcion, Mani and Bardaisan," edited from a palimpsest MS. of the British Museum by C. W. Mitchell, Vol. I., 1912.

composed—light, wind, water, fire and darkness. The elements of the "Socrates" are those traditional in Greek philosophy, except that the Persian term wind is substituted for "air"; those of Bardaisan are Persian and are identical with those of the Manichæans. But Ephraim says ("Adv. Haer.," 41, Vol. II., p. 532, Vatican edition) that Bardaisan regarded darkness as "nothing and capable of nothing." It could not therefore have been in his system, as it was in the Persian and Manichæan, the active principle of evil, but was rather a mere negation, analogous to the Aristotelian substratum, a doctrine which Ephraim repeatedly ascribes to Bardaisan. It may be compared to that fifth something which the "Socrates" speaks of as "that which was undifferentiated and unknown" or "unknowable," although this is not explicitly termed an element.

According to the "Socrates" the animal soul or life is compounded out of the four elements; its nature depends upon the proportions in which the elements are combined and in particular upon the amount of fire present. The animal soul then consists of four parts. At least some human souls consist of the animal plus the rational soul. The latter has three parts, "Greatness," "Power," and "Goodness," which are the first three manifestations of the "Original Root," a term which in this work is clearly equivalent to "God." Thus the rational soul is divine and those human souls which contain it are composed of seven elements or parts. Ephraim's statements about Bardaisan's theory of the soul have hitherto presented insurmountable difficulties, all of which disappear if he be regarded as criticizing the theory of the "Socrates." In one passage ("Adv. Haer.," 54, Vol. II., p. 555) Ephraim says that the soul was "made of the existents." The "existents" must have been four in number, for darkness or negation, as representing unconsciousness, could contribute nothing to soul. Elsewhere, ("Second Discourse to Hypatius," p. 8, 5 sqq., Mitchell), he says that the soul consists, according to Bardaisan, of seven parts. According to the "Socrates" the first of these statements is true of the animal soul, the second of the union of the animal with the rational soul. Ephraim then describes the dependence of the soul's character upon the proportions of the components precisely as is

done in the "Socrates," and adduces two arguments against the theory. First, the souls of angels and devils are unchangeable, whereas this theory makes them changeable. Second, the sun is unchangeable. This second objection seems on the surface quite irrelevant, and there is nothing in Ephraim's text to indicate why he regarded it as an argument against Bardaisan's theory. Turning to the "Socrates" one finds that the author devotes nearly one fourth of the dialogue to drawing a parallel between the changes which the soul undergoes during life and those through which the sun passes in completing his daily and annual course.

The "Socrates" uses for "God" the term "Original Root" or "That Power." The first manifestation of the Root is "Greatness" (*rēbhūthā*), which is probably here equivalent to the Greek *μέγεθος*, a term used in geometry for "extension" and by some Gnostics as a designation of God. It is complementary, so to speak, to "Æon," the more common Gnostic term for God, which means "duration," duration and extension being conceived as the primary expressions of the divine essence. The relation between this "Original Root" and space (*athrā*) is conceived in the "Socrates" as very intimate indeed. "That Space" is said in one passage to "be" the Root, but more commonly space is conceived as anterior to the Root. Thus we are told that "Greatness, Power, and Goodness" "cannot exist in Place but (only) where they have Space that they may be kept in righteousness, refined and pure." And again, "Because the Greatness of this Power is vast [Power], therefore is it in the compass of the All and outside the All, and there exists no empty Space wherein is nought of it." Thus God is placed in space. Ephraim repeatedly charges Bardaisan with making space superior to God and placing God in space, and in one passage ("Against Hypatius," IV., p. 133, 1 Mitchell) he says: "Greater are the praises which Bardaisan uttered concerning space than those which he uttered concerning the God who is in the midst of space." In another (*ibid.*, p. 132, 42): "Therefore the Greatness which the Teachings give to space, the Teachings of Truth give to God." It is noteworthy that the name "God" is sedulously avoided by the author of the "Socrates"; it does not occur even once.

From this mystical theory of the soul's relation to her source the "Socrates" draws some important practical conclusions. Since the rational element is identical in all human souls which possess it and since it is still in organic union with their common Root, it necessarily follows that such souls enjoy a virtual community of knowledge. It is by virtue of this community of knowledge that truth spoken by one receives the assent of another. "But you, Herostrophus," says Socrates, "have not come to ask or inquire of me aught which is not your own. If it be of speech that you would inquire of me, it is in you and is yours; if of sight, it is yours; if, again, of hearing, it is in you. For no man shall see Good except him in whom it is and no man speaks speech unless it be implanted in him nor hears unless it is in him. That through which the eye sees and the ear hears and speech speaks, [and] these three which appear distributed among sense-organs (lit. parts, *i. e.*, *μέρη*)—their Root is one. And all these things which I have said to you, Herostrophus, if you should see them as I do and hear them as I do—and you do (lit., such you are)—the Root is one. And if again in another Space you should hear this discourse which you are hearing from me, know that this is the Root of which is no Space empty where it is not. For we who abide in the Root are like the branches of a tree, some in the east, some in the north, some in the south, some in the west, but the remainder is One Root." Ephraim criticizes ("Against Hypatius," V., p. 159, Mitchell) a precisely similar doctrine: "According to it one soul has no need of another soul to learn or teach . . . because the knowledge of their essence is equal if, as they say, the essence of all souls is one. If Teacher and Teaching (pupil?) are from one Root and both are clad in flesh . . . how does one go astray and another teach? . . . If there is recollection in all the Root, there is no error in all the Essence. And the sons of this Essence (*i. e.*, those who share in the Essence)—how does one fail and another succeed? Their essence is not the same." Ephraim rarely mentions the name of the author he is controverting and in this passage he does not mention Bardaisan. But in these sermons he is criticizing only Marcion, Bardaisan and Mani and as there is no reason for ascribing the doctrine in question

to either of the other two, it is probably to be referred to Bardaisan. And the language and imagery strongly suggest the "Socrates." The author of the "Socrates" draws from his theory the legitimate conclusion that the rational soul only is immortal; the animal soul and the body both perish at death. That Bardaisan denied the orthodox doctrine of the resurrection of the body is agreed by all our authorities.

The agreement between the cosmology of the "Socrates" and that of Bardaisan is not so exact as that subsisting between these two groups of psychological theories, but they present nevertheless some notable points of analogy.

Theodore bar-Koni describes Bardaisan's system as follows (a few additions have been made from Ephraim and Moses bar-Cephā): From eternity God and the five elements coexisted in perfect peace. God was above all, Darkness below all; in between were the other four elements disposed in the same plane—Light in the east, Wind in the west, Water in the north, Fire in the south. Then the Wind blew by chance and beat upon and agitated the elements; a smoke not born of Fire gathered (Ephraim has: Darkness crossed its border upwards). Then God sent an utterance of Thought which arrested the Wind and a Wind from on High quieted them in part. The confused portion was then separated from the others and from it the world was made.

According to the "Socrates" there existed from eternity with "That Power," *i. e.*, God, a something which you may call at pleasure soul or fire or nature (*φύσις*). Since the author has just shown at length that soul consists of the four elements, fire being only the chief among them, and since he immediately proceeds to refer to "the four elements of the powers," *i. e.*, the four elementary properties, as existing, one may infer that the eternal existence of soul implies that of the four elements. The scheme is therefore analogous to that of Bardaisan, save that the latter has the Persian term Wind instead of the Greek Air.

The "Socrates" proceeds: "When that Power wished to exist (or be) in purity all by himself he therefore commanded that Body should become (or, come into being as) the organization of the

whole world. And it was spread out⁶ (?) by him upon that which was undivided (or undifferentiated) and unknown." The strange motive for the construction of the world here ascribed to God—the desire to purify himself of soul or matter—occurs, so far as I know, nowhere else. It is clear from Ephraim's discussions that he knew of no motive assigned by Bardaisan.

In the next stage, according to the "Socrates," "by his Word he agitated her (the soul) and separated her from himself. Then all the things which are now seen were (or, became) commingled one with another without form." The Word or Logos seems to be here represented as the cause of chaos—another strange idea, for in the systems influenced by Stoicism it is usually the function of the Logos to transform chaos into the cosmos. Bardaisan's system agrees with the "Socrates" in recognizing an origination of chaos—which is an unusual trait—but attributes it to chance. Ephraim has preserved ("Against Hypatius," III., p. 69, 40 Mitchell) the very words of his source—"At that very time a cause came to be by chance and the Wind dashed against the Fire."

According to Theodore, the Wind is checked by "an utterance of Thought," the agitation quieted by a Wind (*i. e.*, πνεῦμα) from on high, and the portion of the elements which is still confused is removed from the others and made into the material universe. These steps are not described by the "Socrates." They are obviously derived, as Theodore himself remarks, from the Valentinian Gnosis.

According to the "Socrates," "it was his will that she (soul) should be divided and should coin and constitute bodies (*pagre, i. e.*, animate bodies) out of the four elements of the powers and according to the number of those seven Governors and Servants of his."

⁶ The MS. has as the verb an *Ethpeal* or *Ethpaal* perfect from the root *pšq*. According to Payne-Smith, this verb is used only in *Pael* and *Ethpaal*, and in the active means "make easy," "expound," "translate." These ideas cannot be fitted into the above context. Ryssel translates *und ganz und gar erleichtert (d. h. von fremden Substanzen befreit) werde zu etwas Untheilbaren und Unerkennbaren*. I have emended it to read *'ethpšēṭ*; compare Eusebius "Theophania," p. 12, Lee, where the same verb is used to describe the activity of the Logos in the universe—"Throughout the universe he spread (*pšāṭ*) himself, above in the height, below in the deep, himself, incorporeal, he extended (*mēthah*)."

One may note in passing that the word here used to denote the planets, which I have translated "Governors" (*madhbērāne*), is used in the same sense in the "Book of the Laws."

The "Socrates," then, ascribes the organization and constitution of the universe to the soul, not to the Logos. Ephraim ("Adv. Haer.," III., lines 102-110, 125-134) rails bitterly against Bardaisan for denying the orthodox doctrine that the Logos constructed the universe and asserts that he represented Wisdom as acting as God's agent in the work of creation. Thus the soul of the "Socrates" corresponds to Wisdom in Bardaisan's system.

The cosmology of the "Socrates" resembles, therefore, that of Bardaisan in several important features, especially in denying the orthodox doctrine of creation out of nothing (the words "create," "creation," "creature" do not occur in it at all) and representing the world as made out of eternally existing elements; in recognizing a fifth something, Darkness, which corresponds to the Aristotelian First Matter; in describing the origin of chaos; in regarding the world-process as essentially the resolution of chaos into cosmos; in regarding evil as nothing but the unregulated conflict of eternally existing and opposed attributes. But the two systems differ in other important features, and it is quite certain that the "Socrates" is not the source from which Ephraim and Theodore drew their information about Bardaisan's cosmology.

Postscript.—In view of the uncertainty of accomplishment which in these troubled times attaches to all activities not contributing to the war, I have decided to add to the above paper a brief statement of the conclusions which I had reached when it was written but withheld in anticipation of the new evidence promised by Mr. Mitchell. Limitations of space will permit only brief reference to the sources, but those that are interested will have no difficulty in verifying them.

Bardaisan wrote dialogues against Marcion and others (Euseb., "Hist.," IV., 30) and many other works, some of which may well have been dialogues; the "Socrates" is one of these. It is the source from which Ephraim drew his knowledge of Bardaisan's theory of soul; it manifests in conspicuous degree the "patience and

polite answers to every man" for which Bardaisan's disciples praised him (Philoxenus *ap.* Cureton, "Spicilegium," p. v); its cosmology is closely akin to and in no point inconsistent with that of the chief source.

That the "Oration of Melito" (Cureton, *op. cit.*, pp. 22-31, Syr.) is also the work of Bardaisan is rendered extremely probable by its close affinity to both the "Socrates" and the "Book of the Laws." The "Socrates" teaches that knowledge of God is implicit in every man by virtue of his relation to the "Original Root." In the "Oration" a similar doctrine is both stated in general terms (*e. g.*, compare "Or.," p. 30, 15, with "S." p. 161, 16) and directly applied to the Emperor, *e. g.* (p. 25, 24): "But thou, a free intelligence and cognizant of the truth, enter into thyself;" (p. 27, 14) "Know thyself and thou shalt know God;" (p. 29, 16) "But thou, feeble man, within whom He is and without whom He is and above whom He is." Its relation to the "Book of the Laws" is even closer; with the latter it insists upon the doctrine of free will and makes extensive use of material drawn from the history and customs of foreign nations in the same curious and characteristic way. The Emperor to whom it is addressed is without doubt Caracalla. He was generally known during his life as simply "Antoninus"; he spent the winter of 216-17 in Edessa; he was wont to seek out and consult astrologers, and Bardaisan, who had been an intimate friend of the late king Abgar IV., must have been brought into touch with him. The dialogue on Destiny which Bardaisan dedicated to him, which M. Nau is right in distinguishing from the "Book of the Laws" ("Le Livre des Lois," pp. 11-12), and the "Oration," were probably both among the results of the personal relation thus established. One may also recognize in some of the bold characterizations of the "Oration" leading traits of Caracalla; compare, for example (25, 25), "if they clothe thee in the fashion of a woman remember that thou art a man" with Dio Cassius's description of the effeminate appearance which Caracalla affected while in the East—his removal of his beard at Antioch (Dio, 77, 20) and the barbaric long-robed costume of his own designing which he wore in Mesopotamia (Dio, 78, 3, 3); com-

pare also ("Orat.," p. 27, 26) "Therefore thou rollest thyself upon the ground before demons and shadows and askest vain petitions from one that hath nought to give" (and also p. 29, 25) with Dio's account (77, 15, 5-7) of Caracalla's vain efforts to recover his health by assiduous devotion to the gods.

As regards the bearing of these conclusions upon the hypothesis which I suggested some years ago ("Bardaisan and the Odes of Solomon" in the *Journal of Biblical Literature*, 1911), that the "Odes" were written by Bardaisan, I can only say that no inferences can be drawn until the "Odes" have been given much more careful study than they have yet received. They are certainly more deeply tinged with Valentinian ideas than are the above three works—much more deeply, indeed, than I supposed when I published my first study of the problem—and many of them are as yet but imperfectly understood. I may, however, remark that the references to persecution in the "Odes" (*e. g.*, 5, 8, 29) would be perfectly appropriate to the situation above supposed; especially would the perplexing allusions of the 29th be at last intelligible. The boldness of the "Oration" must have inflamed Caracalla's savage temper to the highest degree and it was no doubt after its delivery that Apollonius, "the friend of Antoninus" (Epiph., "Haer.," 56), demanded of Bardaisan that he renounce his faith, and received an uncompromising refusal. Epiphanius says that on that occasion Bardaisan very nearly attained the rank of a confessor. It is probable that he would have attained the still higher rank of a martyr if Caracalla had not been assassinated, April 8, 217, while making a trip from Edessa to Harran. Compare with this situation the language of the 29th Ode:

- 4 He has raised me from the depth of hell
and from the mouth of death has drawn me;
- 5 I have brought low my enemy
and He has acquitted me by His grace. . . .
- 7 He showed me His sign
and guided me by His light;
He gave me the rod of His power
- 8 that I might subdue the thoughts of the peoples,
to bring low the prowess of warriors,

9 to make war by His word,
to take victory by His might.

10 The Lord cast down my enemy by His word
and he became like the chaff which the wind carries off.

Another scrap of evidence, from a quite different source, points in the same direction. The sixth Ode contains a simile which has caused no little perplexity:

7 For a stream went forth
and became a river great and broad,
8 For it overwhelmed everything
and shattered and brought (them) to the Temple.
9 And the restraints of men could not restrain it
nor the arts of them that restrain waters.

This river, it appears, is the Gospel. But why does the Gospel bring its conquests to the "Temple"? What is the "Temple"? And why this curiously specific allusion to the hydraulic engineers? In the Edessene Chronicle one finds a contemporary account of a flood which devastated Edessa A.D. 201 (*BO*, I., 390-91). A spring within the palace grounds overflowed and inundated the palace. "While the wise men were thinking what they should do to the flood of water which was increasing" a heavy rain came on during the night, the river Daisan overflowed its banks and formed a deep lake which finally overtopped the west wall of the city and poured over the battlements. King Abgar ordered the sluice-gates to be opened, but it was too late—the wall collapsed, the flood destroyed the palace "and the waters swept away everything before them, the fair and beautiful buildings of the city, everything near the river southward and northward, and they also made an onslaught on the temple of the congregation of the Christians." Unfortunately the word used⁷ does not indicate the amount of damage to the "temple" of the Christians, but from the very fact of its ambiguity, following as it does unambiguous words, and from the order of the narrative one may infer that the damage fell short of complete destruction. Manifestly, this is precisely the situation depicted in the Ode—the building used by the Christians of Edessa

⁷ *shw* may signify any amount of injury from a mere attack upon to total destruction.

for their worship was popularly known as their "temple," a great flood which hydraulic engineers had striven in vain to control carried masses of débris up to the doors of that temple. The poet takes the catastrophe, in which more than two thousand persons perished, as a symbol of the triumphal progress of the Gospel which sweeps through the world, overcoming all obstacles, and brings its captives into the Church.

UNIVERSITY OF PENNSYLVANIA,
April 3, 1918.

BIOCHEMICAL STUDIES OF THE PITCHER LIQUOR OF NEPENTHES.

By JOSEPH SAMUEL HEPBURN, A.M., M.S., PH.D.

(Read April 14, 1917.)

As the pitcher of *Nepenthes* gradually develops, a liquor is secreted and occupies the lower portion of its cavity. After the operculum, or lid, has opened, insects are attracted by the nectar which is secreted by glands. The nectar glands are found on the outer surface of the pitcher, more abundantly on the inner surface of the lid, and on the inner edge of the corrugated rim that surrounds the margin of the pitcher. The insects, thus attracted, are tempted down into the pitcher, and pass to a richly glandular zone with a smooth surface—the so-called detentive surface—on which they lose their footing, and are precipitated into the liquor. The insects are then digested by the liquor.

Two theories exist as to the manner in which digestion occurs; each theory is supported by experimental evidence. Hooker,¹ Tait,² von Gorup and Will,³ Vines,⁴ Goebel,⁵ Clautriau,⁶ and Fenner⁷ concluded from their researches that the digestion is due to an enzyme

¹ Hooker, *Nature*, 1874, X., 366-372. Report of the Forty-fourth Meeting of the British Association for the Advancement of Science, 1874; Notes and Abstracts of Miscellaneous Communications to the Sections, 1875, pp. 102-116.

² Tait, *Nature*, 1875, XII., 251-252.

³ von Gorup and Will, *Sitzungsberichte der physikalisch-medizinischen Societät zu Erlangen*, 1875-6, VIII., 152-158. *Ber. der deut. chem. Gesell.*, 1876, IX., 673-678.

⁴ Vines, *Jl. of Linnean Society, Botany*, 1877, XV., 427-431. *Annals of Botany*, 1897, XI., 563-584; 1898, XII., 545-555; 1901, XV., 563-573.

⁵ Goebel, *Pflanzenbiologische Schilderungen*, 1893, II., 186-193.

⁶ Clautriau, *Mémoires couronnés et autres mémoires, publiés par l'Académie Royale des Sciences, des Lettres et des Beaux Arts de Belgique*, Collection in 8°, 1899-1900, LIX., third memoir, 56 pages.

⁷ Fenner, *Flora oder allgemeine botanische Zeitung*, 1904, XCIII., 335-434 (especially pp. 358-363).

present in the pitcher liquor. On the other hand, Dubois⁸ and Tischutkin⁹ concluded from their experiments that the digestion is due to the activity of microörganisms. A third factor to be considered is the autolysis produced by the tissue enzymes of the captured insects.

In the present research, the proteolytic enzyme of the pitcher liquor and the bacteria, which occur in opened pitchers, have been studied separately. The following species and hybrids of *Nepenthes* supplied material for the research: *ampullaria*, *atrosanguinea*, *Chelsonii*, *Claytonii*, *Dominii*, *Dyeriana*, *gracilis*, *Hamiltoniana*, *Henryana*, *Hookeriana*, *Mastersiana*, *mixta*, *Morganiana*, *paradisæ*, *Rafflesiana pallida*, *rufescens*, *splendida*, *Wittei*. The plants were grown in the *Nepenthes House* of the University of Pennsylvania.

PROTEASE OF THE PITCHER LIQUOR.

In the study of the protease of the pitcher liquor, pitchers were always selected prior to opening. They were closely watched and the mouth of each pitcher was closed with absorbent cotton as soon as the lid opened; the entrance of insects was thereby prevented, and possible contamination of the pitcher liquor by the tissue enzymes of the digested prey was entirely excluded. The digestion experiments with the pitcher liquor were made *in vitro* in the presence of a bactericide; bacterial action was thereby excluded. The proteolysis, which was observed, was, therefore, due to enzyme action.

Liquor from both non-stimulated and stimulated pitchers was studied. The experiments on liquor from non-stimulated pitchers were carried out as soon as possible after the opening of the pitchers.

When liquor from stimulated pitchers was desired, recourse was had to mechanical stimulation by chemically inert substances. In some experiments, the glands of the inner wall of the pitcher were stroked repeatedly with a camel's hair brush, and the cotton plug was then inserted in the mouth of the pitcher; the liquor was removed for study on the following day. In other experiments, several round solid glass beads, such as are used in fractionating

⁸ Dubois, *Comptes rend. de l'Academie des Sciences*, 1890, CXI., 315-317.

⁹ Tischutkin, *Botanisches Centralblatt*, 1892, L., 304-305.

columns, were inserted into the newly opened pitcher; the cotton plug was introduced, and the pitcher and its contents were shaken thoroughly at intervals during one or more days, taking care not to wet the cotton and thereby lose liquor; the liquor was finally removed and used in digestion experiments.

The volume of liquor secreted by a single pitcher was always so small that liquor could not be obtained from the same pitcher both before and after stimulation. Since two pitchers rarely matured on the same plant at the same time, it was impossible to make a comparative study of the liquor from both non-stimulated and stimulated pitchers of the same plant. While the differences, due to individual plants, could not be entirely eliminated, the problem was attacked by several methods for the study of proteolysis, and a number of experiments were conducted according to each method; the results obtained by all the methods lead to the same general conclusions.

Either sodium fluoride or trikresol was used as a bactericide in all the experiments reported below. When sodium fluoride was used, sufficient solid fluoride was added to the mixture of pitcher liquor and substrate to render the final concentration of sodium fluoride one per cent. When trikresol was used, a sufficient volume of a two per cent. aqueous solution of trikresol was added to render the final concentration of trikresol 0.2 per cent.—a concentration which was found satisfactory by Graves and Kober¹⁰ in certain of their experiments with proteases. Whenever the mixture of pitcher liquor and substrate was diluted to a definite volume, the trikresol solution was added before the dilution to the final volume was made.

Unless otherwise stated, the temperature of incubation was 37° C.

In each experiment, a blank or control experiment was carried out with pitcher liquor which had previously been boiled, then cooled to the temperature of the room; the control experiment was carried out in exactly the same manner, in all other respects, as the determination proper. The control was always compared with the determination proper; and due allowance was thus made for the

¹⁰ Graves and Kober, *Jl. Am. Chem. Soc.*, 1914, XXXVI., 751-758.

possible action of any thermostable catalyst present in the pitcher liquor, and also for any action of the reagents on each other.

The following reactions for the detection of a protease were used:

1. The formol-titration of Sørensen.
2. The digestion of:
 - (a) Carmine fibrin.
 - (b) Edestan.
 - (c) Protean of castor bean globulin.
 - (d) Ricin (Jacoby).
3. The cleavage of glycytryptophane.

FORMOL-TITRATION.

Composite samples of liquor, obtained from several pitchers, were used, a different sample for each experiment. The indicator was phenolphthalein.

TABLE I.
FORMOL-TITRATION AFTER DIGESTION.

Liquor from	Substrate.	Weight of Substrate, Gram.	Volume of Pitcher Liquor, C.c.	Total Volume of Digestion Mixture, C.c.	Period of Incubation, Days.	Formol-titration after Deduction of Blank,
Non-stimulated pitchers	Ovalbumen . . .	0.05	10.0	10.0	4	0.00 c.c. 0.1 N NaOH
	Nährstoff Heyden*	0.25	12.5	37.5	4	0.00 c.c. 0.1 N NaOH
	Witte peptone..	0.25	12.5	37.5	4	0.00 c.c. 0.1 N NaOH
Stimulated pitchers.	Ovalbumen . . .	0.05	15.0	15.0	3	0.15 c.c. 0.05 N NaOH
	Fibrin	0.05	15.0	15.0	14	0.45 c.c. 0.1 N NaOH
	Ovomucoid . . .	0.05	5.5	15.5	6	0.10 c.c. 0.1 N NaOH
	Nährstoff Heyden*	0.15	15.0	30.0	3	0.20 c.c. 0.1 N NaOH
	Witte peptone..	0.25	25.0	50.0	4	2.75 c.c. 0.1 N NaOH

* According to Gotschlich (Kolle und Wassermann, Handbuch der pathogenen Mikroorganismen, 2 Auflage, 1912, I., 102), Nährstoff Heyden is a mixture of different albumoses.

In the first series of experiments, reported in detail in Table I., the pitcher liquor was permitted to act on a given substrate for the time stated. Undissolved protein was then removed by filtration, and was washed on the filter; the combined filtrate and washings were made neutral in reaction. Any precipitated metaprotein was separated by filtration, and was washed on the filter; the combined filtrate and washings were neutralized, if necessary. One half their volume of a neutral, 40 per cent. formaldehyde solution was then added, and the carboxyl groups of the amino acids were immediately titrated with standard sodium hydroxide solution. It should be noted that no acid was added in the digestion experiments of Table I.

A second series of experiments was carried out with edestan as the substrate; in these experiments, the hydrochloric acid, which was used to convert edestin into edestan, was present in the solution during the digestion. The details are given in Table II.

TABLE II.
FORMOL-TITRATION AFTER DIGESTION OF EDESTAN.

Liquor from	Volume of Pitcher Liquor, C.c.	Weight of Edestin, Gram.	Volume of 0.1 N Hydrochloric Acid, C.c.	Volume of Water, C.c.	Total Volume of Digestion Mixture, C.c.	Period of Incubation, Days.	Formol Titration after Deduction of blank, C.c. 0.1 N NaOH.
Non-stimulated pitchers.....	11.5	0.100	15.0	23.5	50.0	28	0.00
	8.0	0.036	5.4	11.6	25.0	21	0.00
Stimulated pitchers.....	8.0	0.050	7.5	17.5	33.0	25	0.90

In both series of experiments the liquor from *stimulated* pitchers invariably digested the substrate, liberating compounds which were of the nature of amino acids, and responded to the formol-titration. The liquor from *non-stimulated* pitchers did not digest the substrate with the production of such compounds, for the formol-titration invariably was zero.

DIGESTION OF CARMINE FIBRIN.

Two sets of experiments were made using carmine fibrin as the substrate. In both series, the temperature of incubation was that of the room. The liquor from a separate pitcher was used in each

experiment, save in those indicated by an asterisk (*) in the tabulated results. In the latter experiments, composite samples of liquor, obtained from several pitchers, were used.

In the preliminary experiments, the carmine fibrin was swollen in a solution containing 0.2 per cent. hydrochloric acid and 0.2 per cent. trikresol. A definite volume of the resulting jelly was placed in a given volume of pitcher liquor; and sufficient hydrochloric acid (0.6 per cent. solution) and trikresol (2 per cent. solution) were added to produce a concentration of 0.2 per cent. of each of these reagents. The time required for solution of the substrate and other details of each experiment are given in Table III.

TABLE III.

DIGESTION OF GELATINOUS CARMINE FIBRIN BY PITCHER LIQUOR IN THE PRESENCE OF 0.2 PER CENT. HYDROCHLORIC ACID.

Liquor from	Volume of Pitcher Liquor, C.c.	Volume of Carmine Fibrin Jelly, C.c.	Solution of Substrate.	
			Marked in Hours.	Complete in Hours.
Non-stimulated pitchers....	1.50	0.10		13
	*4.75	0.25	31	
Stimulated pitchers.....	1.50	0.10		13
	4.00	0.50	15	24
	4.00	0.50	48	144
	*4.75	0.25		26

In the final series of experiments, 0.2 gram of carmine fibrin was weighed out into a separate tube for each experiment. This series falls into three groups. In group *A*, the carmine fibrin was swollen in its tube in a solution containing 0.2 per cent. hydrochloric acid and 0.2 per cent. trikresol, then was transferred to another tube and immediately used in a digestion experiment. In groups *B* and *C*, unswollen carmine fibrin was used. No hydrochloric acid was used in group *B*; in the other two groups, sufficient 0.6 per cent. hydrochloric acid was added to render the final concentration of that acid 0.2 per cent. Trikresol was used as a bactericide in all three groups, adding sufficient of its 2 per cent. aqueous solution to produce a final concentration of 0.2 per cent. The details of these experiments are recorded in Table IV.

TABLE IV.
TIME REQUIRED FOR DIGESTION OF 0.2 GRAM OF CARMINE FIBRIN
BY THE PITCHER LIQUOR.

Group.	Liquor from	Volume in C.c. of Pitcher Liquor.	Time Required for Com- plete Solution of Substrate.	Reagents Used.
A.	Stimulated pitchers	3.5	48 hours	Swollen carmine fibrin and 0.2% hydrochloric acid
		2.5	72 "	
		2.0	93 "	
		3.5	111 "	
		1.0	133 "	
B.	Non-stimulated pitchers..	1.0	Substrate absolutely unattacked after in- cubation for 70 days	Unswollen carmine fibrin; no hydro- chloric acid
		1.5		
		2.5		
		3.0		
		3.5	Time required for marked digestion of substrate	
		5.5		
C.	Non-stimulated pitchers..	2.5	16 hours	Unswollen carmine fibrin and 0.2% hydrochloric acid
		1.0	52 "	

The results of both series of experiments (Tables III. and IV.) demonstrate that the liquor from both non-stimulated and stimulated pitchers dissolved carmine fibrin in the presence of 0.2 per cent. hydrochloric acid, and that liquor from non-stimulated pitchers had absolutely no digestive action on that substrate in the absence of that acid.

DIGESTION OF EDESTAN.

The solution of edestan was prepared by dissolving 0.1 gram of edestin in 15 c.c. of 0.1 *N* hydrochloric acid, previously diluted with water to a volume of 25 c.c. The details of the various experiments are given in Table V. After incubation of the mixture of pitcher liquor and edestan solution, it was rendered neutral to phenolphthalein by addition of 0.1 *N* sodium hydroxide solution.

In the experiments with liquor from stimulated pitchers, no precipitate formed in the determination proper on neutralization, showing that the digestion of the protean edestan had advanced beyond the metaprotein stage. In the experiments with liquor from non-stimulated pitchers, a precipitate always formed in the

determination proper, but it always was decidedly less voluminous than the precipitate in the corresponding control experiment; therefore digestion of the substrate had occurred, though less rapidly than when liquor from stimulated pitchers was used.

TABLE V.
DIGESTION OF EDESTAN BY THE PITCHER LIQUOR.

Liquor from	Volume of Pitcher Liquor, C.c.	Volume of Edestan Solution, C.c.	Volume of Water, C.c.	Total Volume of Digestion Mixture, C.c.	Period of Incubation, Days.	Precipitate on Neutralization of Experiment Proper After Incubation.
Non-stimulated pitchers...	1	2	2	5	8	Precipitate one half as great as in blank
	4	1	0	5	13	Precipitate one half as great as in blank
Stimulated pitchers.....	20	25	5	50	14	No precipitate
	1	2	2	5	8	No precipitate

DIGESTION OF THE PROTEAN OF CASTOR BEAN GLOBULIN.

A 2 per cent. solution of castor bean globulin in 5 per cent. sodium chloride solution was used. This solution was filtered, if necessary, then mixed with the pitcher liquor; 0.1 *N* hydrochloric acid was next added; a cloudy precipitate of the protean derived from the globulin formed. The presence in the pitcher liquor of a proteolytic enzyme, active in the presence of hydrochloric acid, was shown by the digestion or solution of the protean, the cloudy precipitate gradually becoming less dense, and finally disappearing completely. Liquor from a separate pitcher was used in each experiment; the details are recorded in Table VI. The protean was usually dissolved by the liquor from both non-stimulated and stimulated pitchers.

DIGESTION OF JACOBY'S RICIN.

The reagent was prepared by dissolving 1 gram of Jacoby's ricin and 1.5 grams of sodium chloride in 100 c.c. of water, and filtering, if necessary. The test was carried out by mixing 1 c.c. of pitcher liquor and 3 c.c. of ricin solution, adding 1 c.c. of 0.56 per cent. hydrochloric acid, then incubating. A cloudy precipitate

TABLE VI.

DIGESTION OF THE PROTEAN OF CASTOR BEAN GLOBULIN BY THE PITCHER LIQUOR.

Liquor from	Volume of Pitcher Liquor, C.c.	Volume of Globulin Solution, C.c.	Volume of 0.1 N Hydrochloric Acid, C.c.	Volume of Water, C.c.	Total Volume of Digestion Mixture, C.c.	Digestion.
Non-stimulated pitchers...	0.6	2.0	0.5	1.9	5.0	No digestion at end of 14 days
	2.5	2.0	0.5	0.0	5.0	Protean completely dissolved in 14 hours
	1.0	2.0	0.5	1.0	4.5	Protean almost completely dissolved in 29 hours
	1.0	2.0	0.5	1.0	4.5	Protean completely dissolved in 48 hours
Stimulated pitchers.....	2.5	2.0	0.5	0.0	5.0	Digestion of protean marked on 3d day, advanced on 7th, almost complete on 12th day
	0.5	4.0	1.0	4.5	10.0	Digestion of protean marked on 4th day, almost complete on 9th day

of protean, derived from the ricin, separated on the addition of the acid. By the action of a protease, this precipitate was gradually digested or dissolved.

In one experiment, liquor from a *non-stimulated* pitcher was used; the cloudy precipitate was partially dissolved in two days, but had not entirely disappeared at the end of seven days. In another experiment, liquor from a *stimulated* pitcher was used, the cloudy precipitate was markedly digested in two days. Therefore, liquor from both non-stimulated and stimulated pitchers exerted a proteolytic action on the protean.

CLEAVAGE OF GLYCYLTRYPTOPHANE.

Liquor from stimulated pitchers was permitted to act on glycylyl-tryptophane in the presence of toluene as a bactericide; 10 c.c. of pitcher liquor and 2 c.c. of an aqueous solution of the dipeptide (so-called Ferment diagnosticum) were used. In one experiment,

cleavage of the dipeptide had not occurred after digestion for nine days in the incubator. In a second experiment, after digestion for twenty-one days in the incubator, followed by seven days in the room, a distinctly positive reaction for free tryptophane was obtained by the bromine and acetic acid test. Hence, liquor from stimulated pitchers apparently hydrolyzed glycytryptophane, provided the period of incubation was sufficiently long.

BACTERIA OF THE PITCHER LIQUOR.

The bacteriological study was made in collaboration with E. Quintard St. John. Unopened and opened pitchers were studied separately.

Unopened Pitchers.—Sterile scissors were used in cutting the plant tissues. The prolonged midrib or tendril, which carries the pitcher, was severed; the top portion of the pitcher was rapidly passed through the flame and was immediately cut off. The cut edge of the pitcher was then flamed rapidly; and the liquor was withdrawn at once with a sterile pipette, and plated on plain nutrient agar. After incubation for four days at 37° C., the plates were examined for bacterial growth.

Twelve pitchers were studied in this manner, the liquor from each pitcher being plated separately. Colonies invariably failed to develop on the plates; hence the liquor in unopened pitchers was sterile.

Opened Pitchers.—Partly opened pitchers, which had not been invaded by insects, were used in two experiments. The liquor from each of these pitchers contained a goodly number of bacteria which grew on plain nutrient agar at 37° C.

All the other experiments were conducted on liquor from open, active pitchers in which insect remains were present.

Total Count.—With each of five pitchers, several successive dilutions of the liquor were sown on plain nutrient agar, and the plates were incubated at 37° C. for four days; the colonies were then counted. The number of bacteria per c.c. of pitcher liquor was as low as 48,000 in one pitcher, and as high as 8,000,000 in another pitcher; the other pitchers gave values: 450,000, 1,200,000, and 1,900,000, respectively.

Several of the colonies were studied separately (*a*) by stained smears, and (*b*) by transfers to lactose bile salt broth. All the microorganisms were rod-like, and a few of them contained spores; none of the transfers developed gas; therefore it may be concluded that members of the family *Bacteriaceæ*, other than the colon-aërogenes group were present.

The liquor in an old pitcher, which was becoming brown at the top, gave a count of 104,000 bacteria per c.c.

Liquefaction of Gelatin.—The liquor from each of two pitchers was sown on nutrient gelatin; the bacteria grew and completely liquefied the gelatin in forty-eight hours.

Tests for the Colon-aërogenes Group.—In two experiments, 1 c.c. of liquor from a single pitcher was sown in lactose bile salt bouillon; on incubation at 37° C., gas developed within seventy-two hours, showing the presence of organisms of this group. A composite sample of liquor, collected from several pitchers, was sown in this medium in several successive dilutions, the greatest dilution being 1 : 10,000; gas developed in even the greatest dilution within seventy-two hours, therefore at least 10,000 organisms of the colon-aërogenes group were present in each c.c. of the liquor.

Certain special media were used in the study of the power of the bacteria to digest proteins, and to decompose simple compounds containing carbon and nitrogen. In the preparation of these media, the directions of Crabill and Reed¹¹ were followed with modifications. A stock solution of inorganic salts, containing magnesium, ferrous, potassium, chloride, sulphate, and phosphate ions, was prepared as directed by these authors, and was used in the media.

The liquor from each pitcher was studied separately in all the experiments described below. The temperature of incubation was always 37° C.

Production of Tryptophane and Indol from Protein.—Protein, obtained from aleuronat, gave a purple color with glyoxylic acid and sulphuric acid, and therefore contained a tryptophane group. A medium, containing 0.4 gram protein, 20 c.c. 0.1 *N* sodium hydroxide solution, and 80 c.c. of the stock solution of inorganic salts, was prepared and sterilized. One c.c. of pitcher liquor was sown

¹¹ Crabill and Reed, *Biochem. Bull.*, 1915, IV., 30-44.

in 10 c.c. of the sterile suspension of protein. In one series of eight experiments, indol had not been produced after incubation for ten days. In another series of eight experiments, neither free tryptophane nor indol was present after incubation for twelve days.

Digestion of Proteins by the Bacteria.—The proteins used were: casein, egg albumen, unswollen carmine fibrin, edestin, ricin (Jacoby), protein (prepared from aleuronat). The media were prepared by addition of 2 per cent. of agar and approximately 1 per cent. of *one* of the proteins to the stock solution of inorganic salts, and were then sterilized. The proteins, therefore, served as the sole source of carbon and nitrogen for the bacteria. These media were used in plating experiments, sowing 1 c.c. of pitcher liquor in each plate. Whenever proteolytic bacteria were present in the pitcher liquor, their colonies gradually digested and dissolved the suspended particles of protein over which they grew. The plates were examined at intervals until drying of the media rendered further observation useless. The bacteria grew and colonies developed on the vast majority of the plates, as may be seen by reference to Table VII., which gives certain details of these experiments.

TABLE VII.

DIGESTION OF PROTEIN MEDIA BY BACTERIA, PRESENT IN LIQUOR
OF OPEN PITCHERS.

Protein Used.	Number of Experi- ments Plated.	Number of Experi- ments Show- ing Growth.	Growth Oc- curred in Days.	Digestion Begun Be- tween Days.	Total Period of Incuba- tion Days.
Casein.....	8	7	3	3 to 5	12
Egg albumen.....	15	11	3 to 9		12 to 14
Carmine fibrin.....	6	6	3	5 to 9	9
Edestin.....	4	4	3	3 to 9	12
Ricin.....	3	2	3 to 5	By 9th day	12
Protein (from aleuronat).....	8	8	3	3 to 5	12

The suspended egg albumen was not even partially digested; possibly this was due to the presence of non-coagulable ovomucoid, and its utilization by the bacteria as a source of carbon and nitrogen. The other suspended proteins were gradually digested, the digestion becoming more marked as the period of incubation increased; however, complete digestion and disappearance of the suspended particles had never occurred by the end of this period.

Sufficient liquor was not always obtained from a single pitcher to permit plating on all six media. However, a general tendency was noted that, when the microorganisms present in the pitcher liquor grew on one of these media, they grew on all the media, and usually exerted a visible digestive action on all the proteins.

Production of Basic Compounds.—A study was also made of the formation of basic compounds by the action of the microorganisms on simple organic compounds, which served as the sole source of carbon and nitrogen in the medium. The solid media were prepared by addition to the stock solution of inorganic salts of 2 per cent. of agar, 0.5 per cent. by volume of a 2 per cent. solution of rosolic acid in 60 per cent. alcohol, and *one* of the following compounds: glycocoll (an amino acid), acetamide (an acid amide), asparagin (which is both an amino acid and an acid amide), ammonium lactate (an ammonium salt of an organic acid). One per cent. of asparagin was used, the other compounds in molecular concentration equal to that of the asparagin. These media were always sterilized by the discontinuous method. Plating experiments were made, sowing 1 c.c. of pitcher liquor in each plate. The production of basic compounds by microorganisms growing on these media was indicated by a red color of the medium beneath and surrounding the colony. Sterile plates were always poured as controls, to be used in determining the changes in color of the experiments proper.

The number of experiments plated on each of these media was:

Glycocoll rosolic acid agar.....	7 experiments.
Acetamide rosolic acid agar.....	7 experiments.
Asparagin rosolic acid agar.....	22 experiments.
Ammonium lactate rosolic acid agar.....	7 experiments.

The period of incubation was from ten days to a fortnight, the plates being inspected at intervals until further observation was rendered useless by drying of the media. Colonies developed in all save one of the experiments, the sole exception being a plate of glycocoll rosolic acid agar. The colonies were usually apparent by the third day; though, in a few instances, they grew so slowly that they became apparent only at the tenth day. The organisms always

produced an alkaline reaction, *i. e.*, a reddening of the medium. This red coloration gradually spread from the colonies as centers over the entire plate, and was quite marked, as a general rule, by the third or fifth day. In those experiments in which colonies developed but slowly, the red coloration was noted by the tenth day. Hence the microorganisms produced basic compounds from the substrates. During the last portion of the period of observation, from the tenth to the fourteenth day of incubation, oftentimes the medium changed in reaction and became acid to rosolic acid, nevertheless the colonies themselves remained alkaline.

Included in the above experiments was a group in which the liquor from each of seven pitchers was plated on all four rosolic acid agars—glycocoll, acetamide, asparagin, and ammonium lactate. The bacteria grew and produced an alkaline reaction at about the same rate in all four media. In these experiments, a record was also kept of the odor of the cultures; quite frequently the plates were characterized on the third day by an odor recalling that of ammonia or amines; this odor was rarely present on the tenth day.

Hence the microorganisms were able to utilize glycocoll, acetamide, asparagin, and ammonium lactate, which formed their sole source of carbon and nitrogen, and were able to produce basic nitrogenous compounds from these substrates.

GENERAL SUMMARY.

The following conclusions are based on the chemical studies:

Using the *formol-titration*, it was found that liquor from non-stimulated pitchers lacked proteolytic power, while liquor from stimulated pitchers produced proteolysis of a number of substrates: ovalbumen, fibrin, ovomucoid, Nährstoff Heyden, and Witte peptone. In the presence of very dilute hydrochloric acid, edestan was digested by liquor from stimulated pitchers, but not by that from non-stimulated pitchers.

Carmin *fibrin* was not dissolved by liquor from non-stimulated pitchers in the absence of acid, but was digested and dissolved by the liquor from both non-stimulated and stimulated pitchers when 0.2 per cent. of hydrochloric acid was present in the reaction mixture.

Edestan was digested by the pitcher liquor in the presence of very dilute hydrochloric acid; liquor from stimulated pitchers produced a more rapid digestion than did liquor from non-stimulated pitchers.

Liquor from both non-stimulated and stimulated pitchers usually dissolved the *protean of castor bean globulin* in the presence of very dilute hydrochloric acid.

Jacoby's *ricin* was dissolved by liquor from both non-stimulated and stimulated pitchers in the presence of very dilute hydrochloric acid.

Liquor from stimulated pitchers apparently produced cleavage of *glycyltryptophane*, when the period of incubation was sufficiently long.

Liquor from *non-stimulated* pitchers exerted proteolytic action only in the presence of acid, failing to produce proteolysis in the absence of acid.

Liquor from *stimulated* pitchers exerted proteolytic action in both the presence and the absence of acid.

The manner in which stimulation causes the pitcher liquor to acquire *active* proteolytic power is a field for further research. Stimulation may produce a change in the hydrogen ion concentration¹² and thus render the reaction favorable for the activity of a protease already present in the pitcher liquor; or it may cause the activation of a zymogen already present; or it may give rise to an increased secretion of protease by the glands of the pitcher.

In the presence of acid, certain substrates—especially *edestan*—were digested by liquor from stimulated pitchers more rapidly than by liquor from non-stimulated pitchers.

The following conclusions are drawn from the bacteriological studies:

Liquor taken aseptically from unopened pitchers was sterile.

¹² Since this paper was presented, an abstract of a monograph by Jenny Hempel entitled "Bidrag til Kundskaben om Succulenternes Fysiologi" (Copenhagen, H. Hagerup, 1916, 147 pp.) has appeared in *Physiological Abstracts*, 1917, II., 146 (issued in May, 1917). The following quotation is taken from this abstract. "The sap of the stimulated pitcher of *Nepenthes* gives values for the hydrogen ion concentration greater than 10^{-7} , but unstimulated pitchers give no definite value."

A goodly number of bacteria were present in the liquor of pitchers which had partly opened, but had not yet been invaded by insects.

The bacterial content of the liquor of open active pitchers, which contained insect remains, was quite high—from 48,000 to 8,000,000 per c.c. of liquor; the organisms were rods. These bacteria liquefied gelatin, and formed colonies on solid media (agar) in which the sole source of carbon and nitrogen was either a protein or a simple organic compound. They usually digested the protein (casein, egg albumen, carmine fibrin, edestin, Jacoby's ricin, protein from aleuronat), but at an exceedingly slow rate. They decomposed the simple nitrogenous organic compounds (glycocoll, acetamide, asparagin, ammonium lactate), frequently producing an odor like that of ammonia and amines, and always imparting an alkaline reaction to the medium; this reaction subsequently changed to acid in some experiments, but the colonies always remained alkaline. The bacteria did not produce either tryptophane or indol from aleuronat protein, when sown on a medium in which the latter was the sole source of carbon and nitrogen. Organisms of the colon-aërogenes group were present; on the average, each c.c. of pitcher liquor contained 10,000 organisms of this group.

The chemical and bacteriological studies taken together lead to these conclusions.

The protease of the pitcher liquor is the chief factor in the digestion of the insects in the pitcher. The bacteria, which occur in the liquor of opened pitchers, play merely a secondary part, as is shown by the slowness with which they digested proteins.

The bacteria and the *Nepenthes* plant live in symbiosis; the bacteria obtain their food from the digested insects and assist, to a limited extent, in the digestion of the insects.

The tissue enzymes of the insects, of course, may assist in the digestion by causing the insects' tissues to undergo autolysis.

NOTE ON THE BIOCHEMISTRY OF THE PITCHER LIQUOR OF SARRACENIA.

Closely related to the family *Nepenthaceæ*, with its single genus *Nepenthes*, is the family *Sarraceniaceæ*, consisting of three

genera: *Sarracenia*, *Darlingtonia*, and *Heliamphora*.¹³ The following experiments were made on the pitchers of two species of *Sarracenia*—*flava* and *minor*—by Frank M. Jones, E. Quintard St. John, and the author, and are mentioned in this place, since they indicate that the digestive action in the pitchers of *Sarracenia* is likewise due to a proteolytic enzyme.

Liquor was obtained from unopened pitchers of *Sarracenia flava*, growing in their native habitat, and was used in test-tube experiments. The liquor digested edestan in the presence of very dilute (less than 0.1 per cent.) hydrochloric acid, and rapidly digested carmine fibrin—swollen or unswollen—in the presence of 0.2 per cent. hydrochloric acid, 0.2 per cent. of trikresol being used as a bactericide. Liquor was also obtained from open pitchers; it had been diluted by rain water, but rapidly digested carmine fibrin in the presence of hydrochloric acid and trikresol, the concentration of these reagents being that just stated.

By means of culture experiments, it was determined that the contents of unopened pitchers of *Sarracenia flava* and *Sarracenia minor* (*Sarracenia variolaris*) were bacteriologically sterile.

The contents of opened pitchers of these species, which contained insect remains, were also studied bacteriologically. The test for the liquefaction of gelatin was conducted as directed by Rivas;¹⁴ the medium was liquefied; and both motile and non-motile rod-like microorganisms were recovered from the resulting cultures. The contents of these pitchers were also plated on certain of the special agar media described in the preceding pages. The bacteria grew on casein agar and on protein (from aleuronat) agar, and digested these proteins, but at an exceedingly slow rate. The bacteria also grew on the various rosolic acid agars—glycocoll, acetamide, asparagin, and ammonium lactate—changing the reaction of the medium to alkaline, and producing an odor of ammonia or of bases; on prolonged incubation the reaction changed to acid. Organisms of the colon-aërogenes group were found to be present by their reaction with lactose bile salt bouillon.

¹³ Macfarlane, Engler's Pflanzenreich, 1908; IV., 110, Sarraceniaceæ, 34 Heft; and IV., 111, Nepenthaceæ, 36 Heft.

¹⁴ Rivas, *Jl. Am. Med. Assoc.*, 1908, L., 1492-1495.

These experiments indicate that in *Sarracenia*, as in *Nepenthes*, the protease of the pitcher liquor plays the leading rôle in the digestion of the captured insects. The bacteria of the pitcher liquor have merely a minor rôle; they live in symbiosis with the *Sarracenia* plant, draw their food from the digested insects, and assist to a limited degree in the digestion of these insects. Tissue enzymes of the insects doubtless also participate in the process of digestion.

The author desires to record his deep indebtedness to Dr. John M. MacFarlane, director of the botanic garden and laboratory of this university, for the material and facilities placed at his disposal for the prosecution of this research, during 1914-1916.

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TWIN HYBRIDS FROM CROSSES OF *ÆNOTHERA* LAMARCKIANA AND FRANCISCANA WITH *Æ. PYCNOCARPA*, IN THE F₁ AND F₂.

(PLATES I-IV.)

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(Read April 13, 1917.)

The peculiar behavior of *Ænothera pycnocarpa* and *Æ. nutans* in reciprocal crosses¹ (Atkinson, 1917) led me to undertake reciprocal crosses of these with other species of *Ænothera*. Among the species which were used more attention has been given to *Ænothera lamarckiana* and *Æ. franciscana*.² Seed of the former was obtained from de Vries, of the latter from H. H. Bartlett.

Reciprocal crosses of these two species with *Ænothera nutans* gave results which indicated that twin hybrids were produced in the F₁. The plants were grown as annuals in 1915, so that the observations were made on summer rosettes and on the mature plants. The number of individuals in some of these crosses was few. The broad leaves of *Æ. nutans*, however, resembling in general form and size those of *Æ. lamarckiana* and *franciscana*, made an analysis of the results more difficult and uncertain than in the reciprocal crosses when *Æ. pycnocarpa* was used, since its rosette leaves are narrow and deeply cut over the proximal half.

This paper, therefore, treats only of the reciprocal crosses of *Æ. lamarckiana* and *franciscana*, with *Æ. pycnocarpa*. The pollinations for the reciprocal crosses were made during the season of 1914. The seeds were sown in March, 1915, transplanted to flats or pots in April, and then transplanted to the garden in June. The season was quite rainy until the latter part of August and in Sep-

¹ These *ænothera* studies were undertaken more from the morphological standpoint than from that of plant breeding.

² *Ænothera franciscana* Bartlett, *Rhodora*, 16, 35, 1914. This species, like *Æ. lamarckiana*, is one of the large-flowered, open pollinated species.

tember. A very few of the plants did not pass beyond the rosette stage, and as there were a number in which stem development began late in the season, it was possible to connect the types of rosettes with the types of mature plants.

RECIPROCAL CROSSES OF *ÆNOTHERA LAMARCKIANA* AND *PYCNOCARPA*.

Cultures of 1915, Annual.

Ænothera lamarckiana × *Æ. pycnocarpa* (No. 99).—Including those individuals which did not advance beyond the rosette stage there were between 80 and 90 plants in the F_1 . There was a distinct splitting into two types, *i. e.*, twin hybrids were formed. In certain respects these twin hybrids agree with twin hybrids obtained by de Vries (1913) in crosses of *Æ. lamarckiana* with certain other species. In certain characters they resemble one of the parents but are modified by the other parent. I shall speak of them as the *pycnocarpa* type and the *lamarckiana* type, but there are such a number of strong contrast characters in the two species that the names of the types might with equal reason be reversed, depending on the form character chosen to represent the type. In this case the deeply cut feature of the rosette leaves, present in *pycnocarpa*, serves to mark the *pycnocarpa* type, while the nearly plain, or slightly toothed feature of the rosette leaves of *lamarckiana* serves to indicate the *lamarckiana* type.

Pycnocarpa Type; *Rosettes*.—A rosette of this type obtained in the 1915 cultures is represented in Fig. 1, Pl. 1. The *pycnocarpa* character, cutness of the basal half of the leaves is clearly seen, though they are not so deeply cut as in the rosette leaves of the parent (see Atkinson, 1917, p. 228, Fig. 13). The rosette is strongly modified, however, by the *lamarckiana* characters, convexity and crinkledness of the leaves, and the leaves are a little broader than those of *pycnocarpa*.

Pycnocarpa Type; *Mature Plant*.—There were 54 mature plants of this type in the culture. The width and edge character of the leaves come from *pycnocarpa*. They are long, narrow, more or less furrowed, and rather strongly toothed, more so over the base, as in *pycnocarpa*. The leaves are rather crowded and drooping, but are

more or less crinkled as in *lamarckiana*. The stem tubercles are red. The calyx bud is rather robust, about 3 cm. long by 7–8 mm. stout, tapering slightly, and then abruptly at the base of the tips, and there is considerable red in longitudinal bars. The flowers are large, up to 6.5 cm. broad; petals 25–30 mm. long and 30–35 mm. broad, broadly obovate and emarginate, overlapping or just closing the gap. The pod spikes are rather dense; the pods 3–3.5 cm. long and 6–7 mm. broad, often with red bars.

Lamarckiana Type; Rosettes.—No fully developed rosettes of the *lamarckiana* type appeared in this annual culture. The type of rosette, however, is shown in Fig. 1, Pl. I., from the F_2 culture. As a whole it resembles neither *lamarckiana* nor *pycnocarpa*. An analysis of the rosette, however, reveals a combination of *lamarckiana* and *pycnocarpa* characters. The edge character of the leaves, toothedness, is that of *lamarckiana*, while the narrowness, non-crinkledness and furrowedness are those of *pycnocarpa*.

Lamarckiana Type; Mature Plants.—There were 35 mature plants of this type in the culture. They agree with those of the *lamarckiana* type in the reciprocal cross. The plants (annuals) were 100–110 cm. high. The stems are green, with red tubercles, a few red tubercles also on the young ovaries. The foliage is rather light green. The leaves are rather narrow and long, over the middle part of the stem $15-17 \times 3-3.5$ cm., the edge only slightly toothed. The lower bracts are leaf like, sessile, up to 13 cm. long by 3.5 cm. broad. The calyx buds are usually green, but sometimes with a flush of red in spots, 3–3.5 cm. long by 8 mm. stout at the base, tapering gradually to the apex or somewhat abruptly contracted at the base of the tips. The buds and flowers are intermediate in size between the two parents; petals $32 \times 30-40$ mm. The pod spike is lax.

Enothera pycnocarpa \times *Æ. lamarckiana* (No. 98).—There were approximately 400 plants in this culture. There were 360 of the *lamarckiana* type, which agree in all respects with the *lamarckiana* type of the reciprocal cross. The remaining 39 plants presented two types of flowers, 34 with large flowers and a long fruiting spike 60–70 cm. long; bracts, especially the lower, large and leaf-like, no flush of red observed on the calyx bud, except rarely, the leaves

were strongly toothed, pod spike lax, and tubercles on the stem green. There were three plants distinctly of the *pycnocarpa* type with small flowers, but no red color was observed. All these 39 plants probably belong to the *pycnocarpa* type so far as the rosettes are concerned, as well as edge character of the leaves.

In all of the hybrid types it has been observed that the color is very variable, especially that of the calyx buds. Also it has been observed that there is a variation in size of the flowers, some of the plants having small flowers, others large. I have suspected that there was further splitting of the types in regard to flower size, but it was impossible with the amount of other work on hand to study flower size, or color behavior in either the F_1 or F_2 cultures. The studies have been confined largely to the rosettes, exclusively so in the F_2 . It would be of interest, however, to study carefully flower and color behavior in the F_1 and F_2 hybrids.

One of the very marked differences between the two hybrid types is the length and general habit of the fruiting spike in the annual forms, and this feature in each twin is in strong contrast to the fruiting spikes of the parents. In the *pycnocarpa* type the density of the foliage and broader leaves, or lower bracts, contrast well with the open foliage and narrow leaves, or lower bracts, of the *lamarckiana* type. The relative width of the leaves, and their crinkled, or noncrinkled character, parallels these features in the rosettes of the twins. The differences in length of the fruiting spike were very striking in this annual culture. While this feature has not been carefully analyzed in biennial cultures, I doubt if the variation in biennial cultures is so great. Even in annual cultures I am inclined to believe that the results would vary to some extent with the season, and the time of the year when stem development began. In the reciprocal cross the same features were presented in the fruiting spikes of the twin hybrids.

Cultures of 1916: Biennial.

In the autumn of 1915 seed was harvested from protected plants, of parents, and twin hybrids of the reciprocal crosses except the *pycnocarpa* type of *lamarckiana* \times *pycnocarpa*. The seed was planted in pans during April, 1916, transplanted to 2 inch, or $2\frac{1}{2}$

inch pots in May, and from these set out in the garden in June. Of the 75–100 seedlings of each hybrid type of the reciprocal cross, 50 were transplanted to the garden. A few (12–15) of the parent *pycnocarpa* were grown for comparison, and about 150 of the parent *lamarckiana*. The object in growing them as biennials was to obtain the well-developed autumnal rosettes. In all of the cultures the rosettes were large, well developed and remarkably uniform except for an occasional mutant from the *pycnocarpa* type, and a few mutants from the parent *lamarckiana*.

The F₂ of the pycnocarpa type (pycno × lam) No. 155.—The *pycnocarpa* character, the cutness of the leaves over the basal half, is very pronounced, though it is not so strong as in the parent *pycnocarpa*. The convexity and crinkledness inherited from *lamarckiana* is very striking. The width of the leaves is greater than in the *lamarckiana* type. The type of rosette is well represented in the F₁ of the reciprocal cross (Pl. I, fig. 1).

The F₂ rosettes of the *pycnocarpa* type of the reciprocal cross (*lam* × *pycno*) were identical with those of the *pycno* × *lam* cross, and no photograph was made, but the form of the rosette of this type is shown in Pl. I, fig. 1.

While this hybrid type has been called the *pycnocarpa* type, the rosettes really show more of the *lamarckiana* character than they do of the *pycnocarpa* character. If these twin hybrids were to be named now, I should reverse the names because of the preponderance of *lamarckiana* characters in the rosettes of the *pycnocarpa* type, and the preponderance of *pycnocarpa* characters in the *lamarckiana* type. But as all my notes, numbers and marks on the negatives correspond to the names here employed, it does not seem wise to change at this time. In this connection it is of interest to note that the *pycnocarpa* type throws occasional mutants. The rosettes of the mutants which have thus far appeared are of two types. One appears to be a dwarf of the true *lamarckiana*. The other has very narrow, furrowed leaves, resembling in some respects the *lamarckiana* type of these twins, but is much smaller and the leaf edge rather strongly toothed the entire length. The *pycnocarpa* type of twin, in addition to presenting a predominance of

lamarckiana character in its rosettes, appears also to have the mutating constitution of *lamarckiana*.

The F₂ rosette of the lamarckiana type (pycno × lam.)—The complex of characters expressed in the rosette, derived from both parents, are such that it resembles neither parent. Still the preponderance of characters expressed in the rosette of the *lamarckiana* type of twin comes from *pycnocarpa*. These are the narrow, furrowed, noncrinkled, repand leaves, while the edge character comes from *lamarckiana*. The leaves are light green. It is a striking rosette and the uniformity throughout the entire row was remarkable (see Fig. 2, Pl. I).

The F₂ rosette of the lamarckiana type of the reciprocal cross (lam × pycno)—Its resemblance to the rosette of the *lamarckiana* type of *pycno × lam* is remarkable. The only observable difference is that there is a slight buckling of some of the leaves, a *pycnocarpa* character. In both of these *lamarckiana* types the uniformity of the rosettes in the row was remarkable.

RECIPROCAL CROSSES OF *CENOTHERA FRANCISCANA* AND *PYCNOCARPA*.

Cultures of 1915; Annual.

Eurothera pycnocarpa × C. franciscana (No. 100).—In this culture there were between 170 and 180 individuals. The majority reached maturity, but there were a few of the more tardy ones which formed autumn rosettes. Several of the latter began stem development and advanced far enough so that the rosette types could be correlated with the types presented by the mature plants in which the mature rosette stage was omitted. In the F₁ the progeny splits into two distinct types, corresponding to twin hybrids in the sense of deVries.

Pycnocarpa Type; Rosette.—The rosette of the *pycnocarpa* type is shown in Fig. 4, Pl. II., at the right. The *pycnocarpa* character is shown in the strongly toothed, partially cut margin of the basal portion of the leaves. This rosette is not so large nor so well furnished with leaves as those of the F₂ since the few plants of 1915 annual culture which did not form stems, were belated and did not form such fully mature rosettes.

Pycnocarpa Type; Mature Plants.—There were 13 mature or nearly mature plants of this type in the culture. They were approximately $1\frac{1}{3}$ m. high (about 130 cm.). All of the red color, except the sunburn comes from the *franciscana* parent, as well as the large size of the flowers. The stems are green with a rather strong tinge of red in streaks, but parts exposed to the sun usually become quite red. Red tubercles are present on the stem, branches and ovaries. The lower branches over the base of the stem are 50–60 cm. long. The flowering branches occur from the middle upward. The leaves over the middle portion of the stem are nearly like those of *pycnocarpa*, long, narrow, furrowed, drooping and strongly serrate on the edges, but the midveins are pink. The foliage is dark green. The calyx buds are 3–3.5 cm. long by 6 mm. broad at the base, slightly tapering from the base to the base of the tips, then abruptly or gradually, and with considerable red color in longitudinal bands. When open, the flower spread is 4.5–5 cm. The petals are obovate, strongly emarginate, pale lemon yellow, 20 mm. long by 25 mm. broad. The stamens overlap and nearly reach the tips of the stigmas, or do not quite reach the base of the stigmas. The pods are 3.5 cm. long by 6–7 mm. broad at the base, tapering gradually and evenly to the apex.

Franciscana Type: Rosette.—An F_1 rosette of the *franciscana* type is shown in Fig. 5, Pl. III, left hand, a belated plant of the 1915 culture. The rosettes of the *franciscana* type are very difficult to distinguish from those of *franciscana* itself. In fact I do not believe that I could distinguish them. It is clearly distinguished, however, from its twin, the *pycnocarpa* type of the same cross, at the right hand, Fig. 6, Pl. III. The leaves of this rosette are narrower than the mean, for rosette leaves of *Æ. franciscana*, or for this twin hybrid *franciscana* type, but as this rosette is a belated plant the leaves have not reached their full sizes.

Franciscana Type: Mature Plants.—There were 153 mature plants of this type in the cross. They measure approximately 1 m. high (90–120 cm.). The stems are green with occasionally a faint tinge of pink over the older portion. Red tubercles are present on the stem, branches and ovaries. The fruiting spike is 40–50 cm. long, the bracts long, green, persistent, the lower ones up to 9 cm.

long by 3 cm. broad. The calyx buds are 3-3.5 cm. long by 7-8 mm. broad at the base, tapering gradually to the apex, usually an abundance of red color in the calyx, sometimes with only a faint tinge. The open flowers are 4.5-5 cm. broad, the petals narrowly obovate to cuneate with gaps between them at the base, 20-25 mm. long and broad in the larger flowers. The stamens do not quite reach the base of the stigma, and the stigmas are more slender and longer than in the *pycnocarpa* type. The flowers are more delicate and wilt earlier than those of the *pycnocarpa* type. Pods 4-4.5 cm. long by 7 mm. stout at the base. The leaves are exactly like those of the parent *franciscana*, narrow, long, only slightly furrowed, toothed on the edges, not so drooping as in the *pycnocarpa* type, plane, midvein white, foliage pale green contrasting strongly with the dark green foliage of the *pycnocarpa* type.

The fruiting spikes in these annual F_1 cultures also show a distinct splitting into two types in regard to the length of the spike or fruiting axis.

Oenothera franciscana \times *pycnocarpa* (No. 101).—The reciprocal cross, *Oenothera franciscana* \times *pycnocarpa* gives also a F_1 progeny which splits into two hybrid types. These types are identical with those just described from the cross *pycnocarpa* \times *franciscana*. There were 102 plants of the F_1 , 90 of these belong to the *franciscana* type and 12 to the *pycnocarpa* type. Here as in the reciprocal cross a preponderance of the progeny is of the *franciscana* type.

THE F_2 GENERATIONS.

From the F_1 progeny of the crosses between *Oenothera franciscana* and *pycnocarpa*, seed was saved and sown from three of the hybrid types, the *pycnocarpa* type, and *franciscana* type of twin from the F_1 of *O. pycnocarpa* \times *franciscana*; and from the *pycnocarpa* type of twin in the reciprocal cross. The cultures were carried along parallel with those of the F_2 described above, from crosses between *O. lamarckiana* and *pycnocarpa*. They were grown as biennials, and the rosettes were mature and fully developed in the autumn of 1916.

Pycnocarpa type F_2 No. 157 (*pycno* \times *fran*).—There were 50

plants in the F_2 of this culture. The *pycnocarpa* type is not fixed in the F_1 , but splits in the F_2 into two types, the *pycnocarpa* type and the *franciscana* type. Of the 50 rosettes in the culture, 13 were of the *pycnocarpa* type, and 37 of the *franciscana* type. The two types which result from the splitting of the *pycnocarpa* type in the F_2 are shown in Fig. 7 (=157.33), Pl. IV., *pycnocarpa* type; and in Fig. 8 (=157.10), Pl. IV., *franciscana* type.

*Franciscana type F_2 , No. 158 (*pycno* \times *fran*).*—There were 64 rosettes of this type in the F_2 , all of the *franciscana* type. There is no splitting of the *franciscana* type in the second generation, but the fluctuating variations in the rosettes are quite marked. These variations relate to the size and shape of the leaves, and parallel the fluctuating variations of the leaves in the rosettes of the parent *Oenothera franciscana*.

Of the reciprocal cross (*Oenothera franciscana* \times *pycnocarpa*), only the *pycnocarpa* type twin was grown in the F_2 . There were 42 plants, most of them developed into mature, autumnal rosettes, but in a few premature stem development checked rosette development. Splitting in the second generation occurs here also. There were 39 rosettes of the *franciscana* type and 4 of the *pycnocarpa* type.

Fluctuating Variations in the F_2 Hybrid Types.—In the second generation in all of the hybrid types of the crosses between *O. franciscana* and *pycnocarpa* the fluctuating variations as shown by the rosettes were very marked. These variations were studied more carefully in the *franciscana* types. It was possible to recognize several groups into which the principal variations could be assembled, although the limits of variation in the several groups were not clear cut. The groupings are as follows:

Series No. 157, F_2 of *pycnocarpa* type (*pycno* \times *fran*). In the splitting between the 50 plants in this culture there were 15 of the *pycnocarpa* type and 30 of the *franciscana* type. The groups of variation in the *franciscana* type, with the number of rosettes in each group, are as follows.

1. Leaves medium broad, dark green, white-veined, 3.
2. Leaves broad, dark green, crinkled, pink-veined, 17 (6 of them rather narrow leaved).
3. Leaves narrow, dark green, white-veined, 4.

4. Leaves broad, dark green, white-veined, 5.
5. Leaves narrow, pale or yellowish green, pink-veined, 6.
6. Leaves narrow, dark green, pink-veined, 2.

Series No. 156, F_2 of *pycnocarpa* type (*fran* \times *pycno*). In the splitting between the 43 plants in this culture there were 4 of the *pycnocarpa* type and 39 of the *franciscana* type. The groups of variation in the *franciscana* type, with the number of rosettes in each group, are as follows:

1. Leaves broad, dark green, crinkled, pink-veined, 4.
2. Leaves broad, dark green, white-veined, 16.
3. Leaves medium broad, dark green, white-veined, 15.
4. Leaves narrow, pale green to yellowish, pink-veined, 3.
5. Leaves medium broad, pale green, white-veined, 1.

Series No. 158, F_2 of *franciscana* type (*pycno* \times *fran*). There is no splitting of the *franciscana* twin in the F_2 . There were 67 plants in the culture. The groups of variations in the rosettes of the second generation of the *franciscana* twin, with the number of rosettes in each group, are as follows:

1. Leaves broad, dark green, pink-veined, 9.
2. Leaves broad, dark green, white-veined, 14.
3. Leaves narrow, dark green, white-veined, 13.
4. Leaves medium broad, dark green, white-veined, 25.
5. Leaves narrow, pale green or yellowish olive green, 3.
6. Leaves narrow, pale green, pink-veined, 2.

Considerable fluctuating variations were presented by the rosettes of the *pycnocarpa* types in the F_2 of the reciprocal crosses. Parallel fluctuations undoubtedly occur in the rosettes of the F_1 of the two types of hybrids in the reciprocal crosses, but as the F_1 plants grown were nearly all annuals the number of rosettes was not sufficient for a study of these variations in the first generation. Since the rosettes of *Oenothera pycnocarpa* are very uniform, the pronounced fluctuating variations in the hybrids of the crosses between *pycnocarpa* and *franciscana* are traceable to the constitution of *Oe. franciscana*, for the fluctuating variations in the rosettes of the *franciscana* hybrid type are parallel with the fluctuating variations in the rosettes of *franciscana* itself. In the 1916 cultures, 135 rosettes of *Oe. franciscana* were grown in the garden as a parallel

culture. Five or six different groups were recognized, but no record was kept of the number of rosettes which could be assigned to each group. The groups are as follows:

1. Leaves broad, dark green, plain, white-veined.
2. Leaves broad, dark green, crinkled, white-veined.
3. Leaves narrow, dark green, red-veined.
4. Leaves, broad, dark green, red-veined.
5. Leaves medium broad, dark green, white-veined.

These marked fluctuating variations in leaf form, representing one of the features in the constitution of *Ænothera franciscana* which is inherited in its hybrid progeny, marks this species as a favorable one for stimulating great fluctuating variations in the hybrids from crosses with other species, indicated not only by the crosses of *Ænothera franciscana*^a and *pycnocarpa* described here but also by the great fluctuating variations resulting from crosses between *Ænothera franciscana* and *Æ. biennis* as described by Davis (1916).

The marked fluctuating variations in the twin hybrids of the reciprocal crosses between *Æ. franciscana* and *Æ. pycnocarpa* might be interpreted by some as indicating that two distinct hybrid types were not present, but that the two forms represent merely a single, wide range of fluctuating variation. That this interpretation is not valid is shown by the fact that the *franciscana* twin type, although variable, is fixed, it does not split in the second generation nor in its fluctuations does it produce typical *pycnocarpa* twin forms; while the *pycnocarpa* twin type splits in the second generation into the two types.

Further evidence that the interpretation given, in this paper, to the results of these crosses, so far as the production of twin hybrids, and one-sided splitting is concerned, is admissible, is found in the very close genetic relation which *Ænothera franciscana* bears to *Ænothera hookeri* (see Bartlett, 1914, p. 33). Reciprocal crosses of *Æ. hookeri* with *Æ. lamarckiana*, or with certain of its mutants,

^a The seed of *Ænothera franciscana* which I have used came from Dr. H. H. Bartlett in the winter of 1914, from a series of cultures which he had continued for a few years, and as I understand it has the same pedigree as the seed employed by Dr. Davis in his interesting crosses with *Æ. biennis*.

give twin hybrids in the first generation, with splitting of one of the twins in the second generation (de Vries, 1913, p. 131). The results of reciprocal crosses of *Æ. franciscana* with *Æ. pycnocarpa* are a close parallel, and indicate that the genetic constitutions of *Æ. franciscana* and *Æ. hookeri* are very similar.

SUMMARY AND CONCLUSION.

The history of the progeny of the crosses of *Oenothera lamarckiana* and *Æ. franciscana* with *Æ. pycnocarpa* belongs in the series of some of the most interesting phenomena of hybridization known in the *Oenotheras*, and discovered by de Vries (1907, 1908, 1909, 1913). These phenomena are, first, the production of twin hybrids in the first generation of a cross, the two hybrids being fixed in the F_1 generation and continuing to reproduce themselves in the F_2 and succeeding generation; and, second, the production of twin hybrids in the F_1 with one-sided splitting in the F_2 , and succeeding generations. In the second case one of the twin hybrids of the first generation is fixed in the F_1 , the other splits in the F_2 , into two types, like the twins of the F_1 , one of which is fixed while the other splits in the F_3 and so on. In the crosses of *Oenothera lamarckiana* and *Æ. franciscana* with *Æ. pycnocarpa*, the cultures have not been carried beyond the second generation. But the existence of this peculiar phenomenon of inheritance in certain crosses among the evening primroses has been so thoroughly demonstrated by de Vries for several succeeding generations that there can be no reasonable doubt that it applies also to the behavior of the crosses here described, for succeeding generations.

In the reciprocal crosses of *Æ. lamarckiana* with *Æ. pycnocarpa* the twin hybrids are fixed in the first generation, and "breed true" in the second, and in all probability, in succeeding generations. Each of the twin hybrids is very uniform, at least in the rosette stage, and shows a minimum of fluctuating variations. The *pycnocarpa* twin type is a physiological homozygote but its fundamental heterozygotic constitution is now and then manifested by the saltatory production of *lamarckiana* forms, and also of forms approaching *pycnocarpa*, or the *lamarckiana* twin type. The reaction system

established in the F_1 zygote which produces the *pycnocarpa* twin type, is in a very high percentage of cases stable in the F_2 and the following generations. But occasionally other reaction systems, usually dormant, are activated, resulting in *lamarckiana*, and other forms. The *lamarckiana* twin type presents also a minimum of fluctuating variations in the rosette stage, though it appears to me probable that it is a physiological homozygote and carries in a latent, or inactive condition the other factors of both parents which are not manifest in the phænotype.

In the reciprocal crosses of *Oenothera franciscana* with *O. pycnocarpa*, only one of the twin hybrids (*franciscana* type) is fixed in the first generation.⁴ The other (*pycnocarpa* type) having a "hybrid constitution" splits in the second generation into two types which are like the twins of the F_1 . The *pycnocarpa* type with great probability would continue to split in the same way in succeeding generations. When the reaction systems of *O. franciscana* and *O. pycnocarpa* meet in egg or F_1 zygote, a new reaction system is established combining the factors of the two parents. In the unions certain factors of one or the other parent preponderate but their influence is modified more or less by the homologous factors. But the new reaction system established in the F_1 zygote is not the same in all the zygotes. As the two different parent reaction systems meet in the egg, one or the other of two new reaction systems is organized, and chance seems to determine which one of these working systems is established in a given zygote. The reaction system of the *lamarckiana* twin is stable, that of the *pycnocarpa* twin is unstable (and heterozygotic). The twin hybrids in these crosses display in the organization of their reaction systems in the F_1 zygote what I have termed "selective dominance" (Atkinson, 1917, p. 253).

I wish here to express my appreciation of aid given by Mr. H. E. Stork, assistant in botany, in writing notes in the field from my dictation, and for making some of the photographs.

⁴ The *franciscana* twin probably carries the *pycnocarpa* factors also, but in a subordinate or permanently latent condition. If so, it is a physiological homozygote. If it were possible to introduce a splitting factor into the *franciscana* twin by an appropriate cross, and cause the *pycnocarpa* character to reappear in some of the progeny, it would indicate the fundamental heterozygotic constitution of the *franciscana* twin.

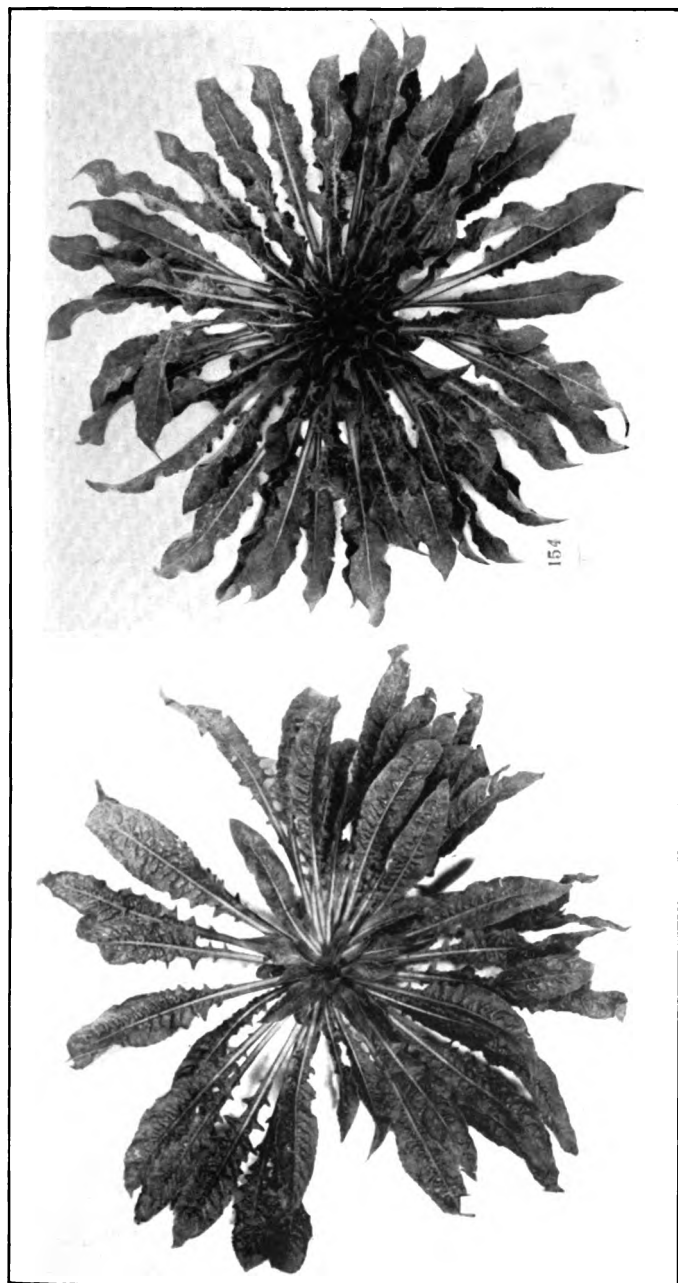


PLATE I.

First generation of cross *Enothera lamarkiana* \times *E. pycnocarpa*.

FIG. 1. *Pycnocarpa* twin type; a belated plant, rosette not fully mature but characters well shown. FIG. 2 (= 154). *E. pycnocarpa* \times *E. lamarkiana*, second generation of *lamarkiana* twin type.

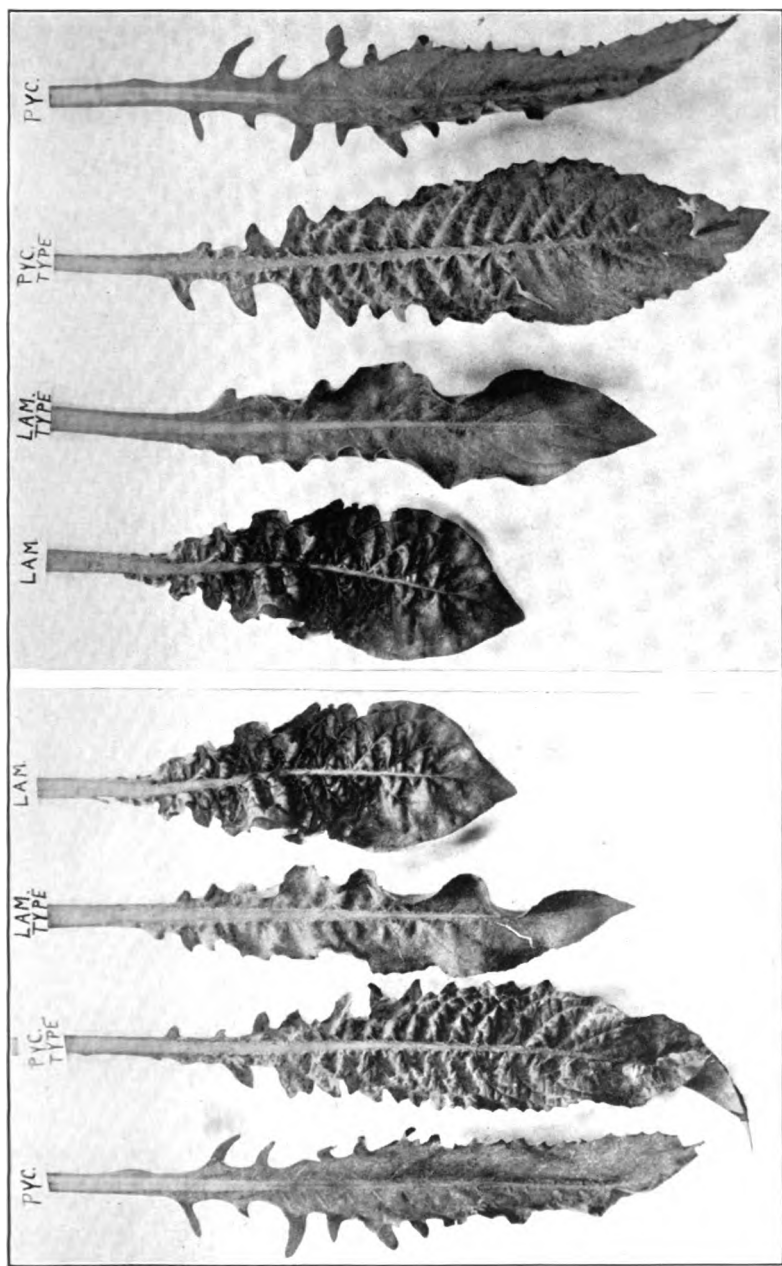


PLATE II.

FIG. 3. *Æ. pycnocarpa* × *Æ. lamarckiana*, with the twin hybrids of the second generation, typical rosette leaves.

FIG. 4. *Æ. lamarckiana* × *Æ. pycnocarpa*, with the twin hybrids of the second generation, typical rosette leaves.

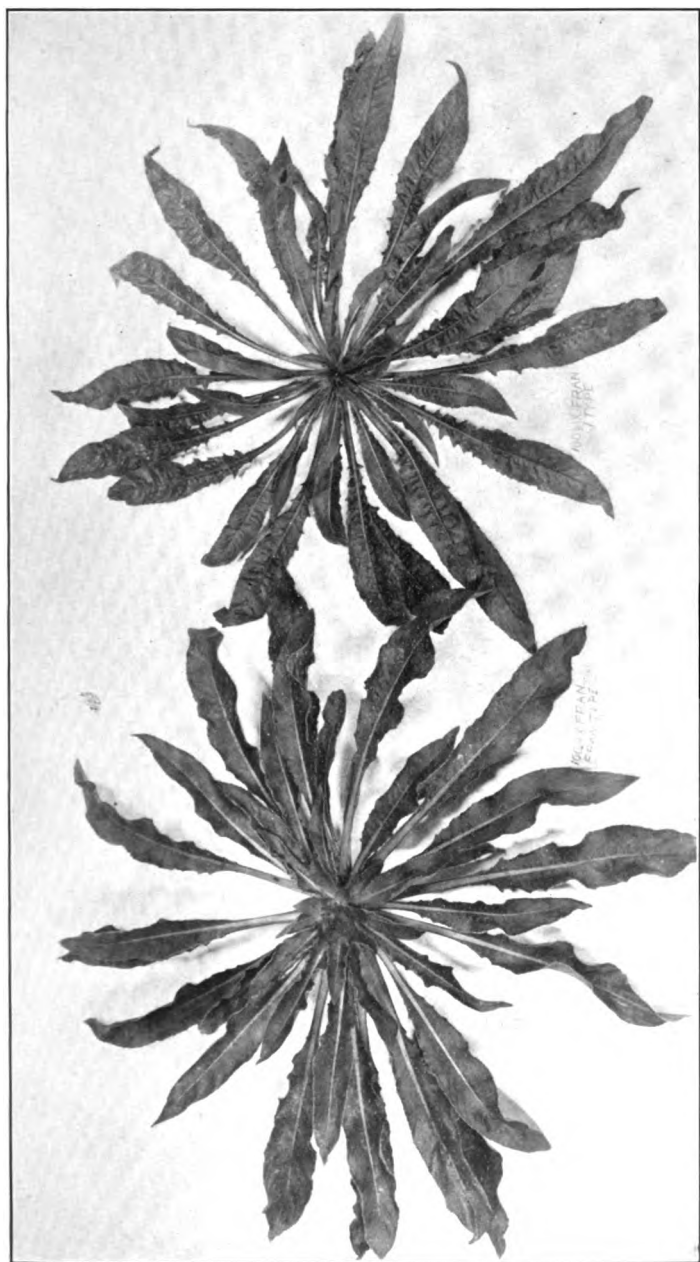


PLATE III.

Enothera pycnocarpa \times *E. franciscana*, rosettes of twins in first generation, belated plants and rosettes not quite mature, but characters well shown.

FIG. 5. *Pycnocarpa* twin type.

FIG. 6. *Franciscana* twin type.

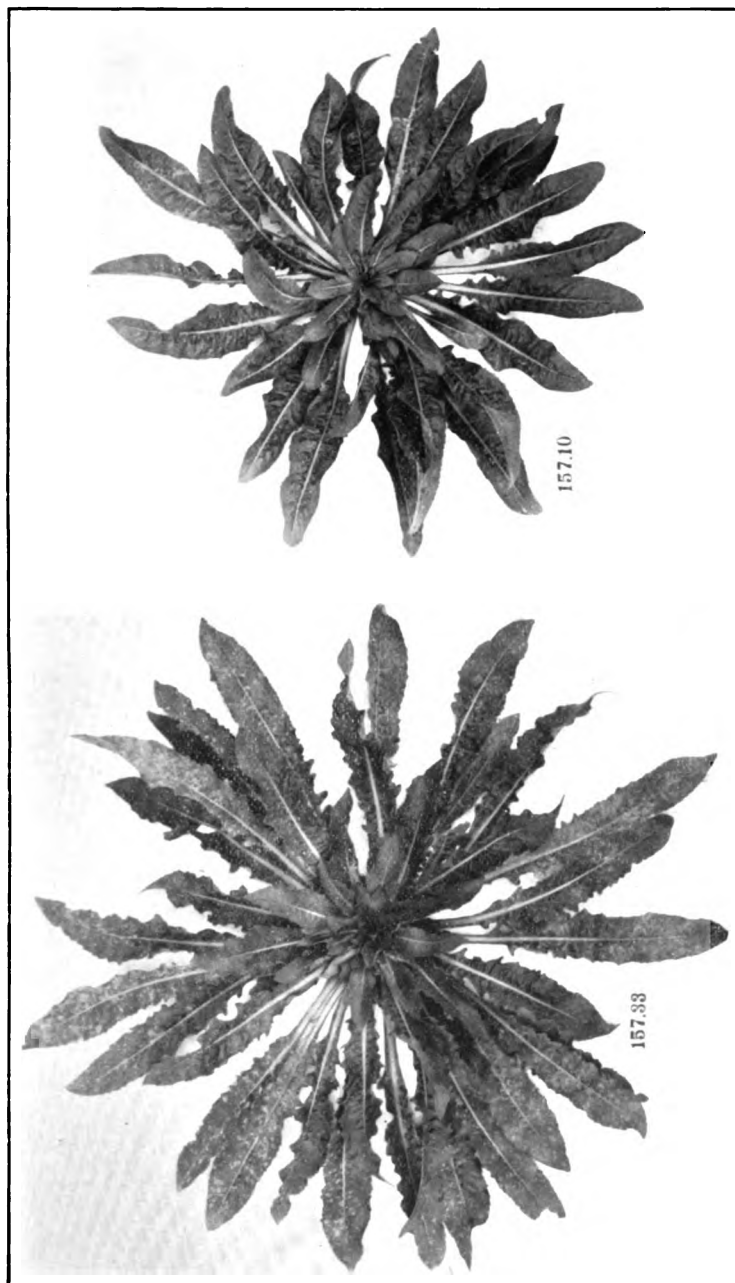


PLATE IV.

Ci. pycnocarpa × *Ci. franciscana*: splitting of *pycnocarpa* twin in the second generation.

FIG. 7 (= 157.33). *Pycnocarpa* twin type.

FIG. 8 (= 157.10). *Franciscana* twin type.

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THE ART OF GEORGE CATLIN.

By EDWIN SWIFT BALCH.

(Read April 19, 1918.)

Within the past decade, a number of American painters have transferred their Lares and Penates from Europe and the eastern United States to Arizona and New Mexico. They have done this because it has dawned on them that the American Indian of the southwestern states offers a splendid opportunity to put on canvas subjects virgin in form and color. About a dozen pictures of Arizona and New Mexico Indians by these painters were in this year's exhibition of the Pennsylvania Academy of Fine Arts. The aim of these painters is undoubtedly artistic, but their works have an important scientific attribute, namely that they record ethnological subjects and in time will form a grand series of illustrations of the appearance and the customs of a few tribes of the original inhabitants of America. About this movement, Mr. Edgar L. Hewett, Director of the School of American Research, Museum of New Mexico, Santa Fe, on the 4th of January last, gave a most interesting account to the American Philosophical Society.

But this movement, important as it is, can do only certain things. The artists of to-day can perpetuate from actual observation only the Indians of to-day. In the United States, they can record the appearance and the doings of the Indians of the desiccated regions of the southwest, whom one may call generically the Pueblo Indians; and even those Indians have had their costume affected by that of the White Race. But they cannot record the historical Neolithic Indian. For the Indian of the Allegheny forest, of the Plains, and of the Rocky Mountains, the Indian of the deer, the bison and the grizzly bear horizon, is a thing of the past. In his genuine native trappings, he can never be painted again.

Fortunately for ethnology and for the history of the natives of America, a handful of painters of by-gone days have left us some

drawings and paintings which form a precious record of our copper-colored predecessors before they had become largely Europeanized. A number of these paintings are in the United States National Museum in Washington, a number are in the American Museum of Natural History in New York, a few are in the Harvard University Peabody Museum and others are scattered throughout the country. Many of these paintings are portraits, usually not of any great art merit. As works of art they will doubtless be greatly surpassed by some of the pictures now being painted. But as ethnological data they are exceedingly important and will always hold their own.

One of these painters of Indians was J. O. Lewis, who painted a good many portraits of chiefs of various tribes, Sioux, Winnebagoes, Chippewas, etc., and who published a portfolio of colored lithographs of them.¹ Many of his models were garbed in a hybrid European dress and the lithographs are too poor to render accurately the heads.

Another painter of Indian portraits was C. B. King. Some of his paintings were reproduced by colored lithography in McKenney's and Hall's book² and historically they are of importance. The frontispiece of the book by P. Rinetisbacher (in text Rhinedesbacher) is an interesting picture of an Indian dance.

One amateur artist who portrayed sporadically Indians was Captain Sully, U. S. A., son of the portrait painter Thomas Sully. In a lecture before the Historical Society of Pennsylvania, on January 14, 1918, Mr. Henry Budd stated that Captain Sully while on frontier duty made some sketches of Indian life.

Captain S. Eastman, U. S. A., made a number of drawings of Indian scenes, which were engraved for Schoolcraft's great work.³ Some of these were from his own sketches, apparently made while he was on active service along the frontier. But some of his drawings were from sketches by other persons, Schoolcraft himself, Lt.

¹ J. O. Lewis, "The Aboriginal Portfolio," Philadelphia, 1835.

² Thomas L. McKenney and James Hall, "History of the Indian Tribes of North America," Philadelphia, 1836, 1842, 1844.

³ Henry R. Schoolcraft, "Historical . . . Information . . . Respecting the History . . . of the Indian Tribes," etc. Illustrated by S. Eastman, Capt. U. S. A., Philadelphia, 1851.

Col. J. H. Eaton, U. S. A., R. H. Kern, Esq., etc. It is not surprising therefore that the engravings are somewhat monotonous in handling and lack to some extent realistic detail. The drawings doubtless were much better than the reproductions, but these nevertheless have saved a great deal which has now passed away of the life of the American Indians and Eastman's work will remain a permanent contribution to American Ethnology.

But by all odds the most important of all painters of the American Indians is George Catlin. Catlin was a man of many activities: a great traveler and something of an explorer, an ethnologist, a geologist, a voluminous writer, but above all a painter. About his travels and his views on geology and ethnology, his own writings offer all necessary data to a student; of his art, numerous engraved reproductions are accessible. But of his art, from a painter's point of view, and of his rank as an artist, no critical study, to my knowledge, has yet been made. And to fill this lacuna by a technical examination of the paintings of this remarkable man is the object of this paper, which although it appears in my name, is really a case of joint authorship. For my wife studied the Catlin pictures in New York and Washington with me and many of the observations and ideas here presented are hers.

I had the pleasure of meeting Catlin on one occasion many years ago in Europe, I think in 1871. He was then traveling about exhibiting his collection of pictures. I went to see these and was lucky enough to find him in the gallery where they were and to have a long talk with him, and I remember him as a most interesting and friendly old man, who loomed up to my boyish eyes as a hero.

Catlin was born in 1796 in the Wyoming Valley, Pennsylvania. His boyhood was passed principally in hunting and fishing. When he grew up he studied law, but soon grew tired of this and went to Philadelphia, where he started as a painter, without teacher or adviser. After several years, one day a delegation of Indians from the "Far West," arrayed in their native dress, happened to pass through the city, and this event determined the course of Catlin's life. He dreamed of nothing but painting Indians and he carried out his dream.

He started in 1832 and wandered all over the plains as far as the Rocky Mountains, living with the Indians for nine or ten years and all the while painting their portraits and making pictures of all the different phases of their life. For some years after this he was occupied in exhibiting these pictures in America and Europe, and also in writing and publishing several important books.⁴ In the "fifties" he traveled extensively in South America, principally in the regions of the Orinoco and the lower Amazon, where his brush once more was ceaselessly busy. After this again he wrote numerous valuable contributions to the knowledge of the Indians of North America and South America and also traveled about exhibiting his collection. After his death, the greater part of his pictures fortunately passed into the possession of the Smithsonian Institution in Washington and of the American Museum of Natural History in New York City.

Almost all of the hundreds of pictures painted by Catlin are of the same size, about 19 by 25 inches. Almost all are painted lengthwise, not upright. In his more elaborate compositions he covered the entire surface. But in many cases he painted an oval picture, which he framed with a black line. He may have used the oval shape because he recognized either consciously or unconsciously that the eyes do really see an oval rather than a rectangle; or because he thereby avoided certain difficulties in filling corners; or he may have found that the oval shape sometimes assisted the composition;

⁴ Catlin's most important publications are as follows:

"Catlin's North American Indian Portfolio," London, 1844.

"Letters and Notes on the Manners, Customs and Condition of the North American Indians," New York, 1844.

"Illustrations of the Manners, Customs and Condition of the North American Indians," London, 1845-1848.

"Life Amongst the Indians," 1861.

"Illustrations of the Manners, Customs and Condition of the North American Indians," London, 1866.

"Last Rambles amongst the Indians of the Rocky Mountains and the Andes," New York, 1867.

"O-Kee-Pa: a Religious Ceremony and other Customs of the Mandans," Philadelphia, 1867.

"Catlin's Notes of Eight Years' Travel and Residence in Europe," New York, 1867.

"North and South American Indians. Catalogue," etc., New York, Baker and Godwin, 1871.

or in some cases he may have saved time which in painting at high speed in the wilds must frequently have been precious.

Most of Catlin's pictures are on prepared paper of a light grayish brown, which often helps a good deal as an undercolor, occasionally remaining untouched. The pictures, as a rule, are light but not bright in tone; there are few brilliant lights and few deep darks; they are usually in a high middle, somewhat dull, register.

Catlin's palette is limited but complete. All the essential colors are on it. The bright colors are used most sparingly and only in small touches and accents. There is certainly white lead. Yellow ochre is much used. A little bright yellow, which may be Naples yellow. Light red. A few touches of two bright reds, almost surely vermilion and rose madder. One bright blue, which almost certainly is cobalt. In one or two cases, in night effects, there seems to be some darker blue, possibly indigo. Brown, probably Vandyke and umber, is a good deal used. Black is occasionally employed and sometimes in night effects pure or nearly pure. There is much dull, usually light green in Catlin's pictures: this may well be a mixture rather than a pure pigment.

The method of Catlin in laying on the paint is of interest. The paint is thin and smooth. It is all applied evenly in one thin coat without retouches. There is no impasto; there are no *repentirs*. His work might almost be called tinted drawing rather than painting. There are two explanations of this mode of work. One of them is that it was to a great extent the method then in use. The painters covered their canvas with a slick surface of paint, from which all roughnesses and ridges were removed. The other cause probably is the great difficulty Catlin must have had in carrying materials and paints with him. He must have opened his colors on his palette in the smallest possible amounts, and made every speck of paint do as much covering as possible.

One of the curiosities of the Catlin collections at Washington and at New York, is that there are no sketch books, no rough drawings, no slips of paper with pencil or chalk marks or blots of water color. Catlin does speak in connection with his first bison hunt, of making drawings of an old bull from his horse in his sketch book, and in another place he writes of altering the finished portrait of a

dissatisfied Indian with water colors; but no such sketches in either pencil or water color, as far as I know, have come down to us. All his works are small finished pictures, which Catlin carried as far forward as he knew how. And considering how well understood his pictures are as a whole, it is astonishing how much detail he gets into his figures and their accessories. But while this multiplicity of detail always takes its position in the whole, as a result his pictures do not carry any great distance; they are best looked at close by. Some of his detail is minute and delicate. Details on the dresses in his portraits are beautifully carried out; there is the greatest delicacy of touch. And it is of ethnographic significance that all the decorations he depicts on the clothing of the figures or on the teepees are always square or rectangular decorations, such as one sees on the Lewis and Clarke skin robe in the Harvard University Museum.

Catlin drew well; not academically but accurately. His portrait heads and full-length portraits may be ranked as fair examples of the style of portraiture in vogue in America in the first half of the nineteenth century. Had he continued painting portraits at home he would doubtless have earned a comfortable competency. And while, of course, Catlin never painted any pictures of architecture requiring linear perspective, his pictures always have the correct artistic perspective which all good landscape painters obtain through intelligent drawing.

A strong point of Catlin is his splendid sense of proportions. He got the natural proportions of figures. His figures are utterly unacademic. He was not preoccupied with Greek or modern European conventional canons of what a human should be. His nudes are nudes, the real thing; they have much the feeling of the French primitives of the Middle Ages. Catlin merely tried successfully to make humans look like what they are, and one feels that nobody looked over his shoulder and told him he was not right.

While all of Catlin's models are copper-colored with straight black hair and sometimes are daubed over with red ochre or other colored earth, nevertheless there are two variations in type. One of these, which is most apparent in the portraits, has features very similar to the Americanized European whose ancestors came over

early in Colonial times and this type resembles the thin gaunt American type of to-day. The other type, which is most apparent in the incident pictures, resembles the Mongol type, both in the faces and in the figures, which are decidedly squat. The latter type often suggests the faces in Aztec or Maya art. Mr. Huntington Wilson, former assistant Secretary of State, tells me that he observed two types among the Indians of South America, one on the high Andes, the other in the hot forest lowlands east of the Andes. Apparently Catlin observed something of the kind among the Indians of the Northern Plains.

Color and also values, that is light and shade, Catlin gets very realistically. He never attempted to solve any artistic problem in color nor in light and shade; he simply painted his subjects straightforwardly and quickly as well as he could. He was absolutely sincere in trying to render what he saw. In the real sense of the word, therefore, his works are genuine realistic impressions. But they have not a semblance of so-called impressionism. His lines, values and colors are always an attempt to present as nearly as he could a scene in nature. His color is sober. Evidently he thought much of local color and little of artistic color schemes. There is no decorative quality in his work. The true function of decorative painting is to make patterns of lines and patches of colors into decorations, not to represent or imitate nature. And there are no line patterns nor patches of color work in any of Catlin's pictures. What he does get in his coloring is a most remarkably faithful rendition of the colors of nature.

The accurate rendition of the colors of nature is shown forcibly in some of Catlin's pictures of South American forests. In them he shows great nerve in tackling the, from our usual pictorial standpoint, utterly unpictorial subjects of the swamps and jungles, whose color might be called a vegetable green monochrome. He suggests the soggy, the pestilential malarial character of these South American swamps in a wonderful way. His forests give the impression of forests, his trees really look like trees in a forest, much more so than does much of the more learned work of the later European painters, then for instance, the forests of some of the Barbizon men or of some of the impressionists. And he succeeds,

largely because he is not afraid of covering a canvas with a mass of green, and because that green does imitate closely the color of a mass of green leaves.

Values Catlin always tried for and usually got very fairly. It is partly because his numerous detail is in value and stays in place that he gives the impression of simplicity and a look of out of doors. He often suggests most successfully distance and atmosphere, as for instance in a picture, now in the American Museum, of some snow mountains, probably the Andes, in which the mountains seem miles away. Some of his skies also, especially at sunrise and sunset, have not only color and light, but most delicate values. To *chiaroscuro*, that is to an artistic arrangement of light and shade or values, he paid less heed. He sought values and sometimes obtained arrangements of light and shade which are most artistic, but it seems always as if it were the subject which bore them in itself, rather than that he was searching for them.

While there is little striving after effect in Catlin's work, still sometimes he painted some memory effects most successfully. Among his *œuvre* are a certain number of night effects, forerunners of our modern nocturnes but not just a dark blue smudge like some of these. They are painted with a generous use of black. There is lots of detail in them: the more you look into them the more you see. Two of these nocturnes in the American Museum may be instanced. One is a camp fire under pine trees which is excellent in composition and in which the pine trees are really drawn. The other is a South American river with some men standing over a lot of captured turtles and a number of women running up waving torches with the most splendid action and motion.

Evidently an inborn gift for composition was one of Catlin's artistic attributes, for he received as little outside artistic influence as any painter ever did, yet each of his pictures shows a distinct power of composing every subject. He had the dramatic instinct, he knew how to place on canvas a scene he had observed so as to make it into a picture. In some of his works, he renders the appearance of a crowd, of a multitude of animated beings, whether Indians, or bison, or peccaries, in a way few painters have done. In his pictures of Indian games, one feels as if there were hundreds

of Indians before one; in his bison hunts, the bison herds stream over the prairies by the thousand. It is largely Catlin's power of composition and selection which makes these pictures successful; indeed almost invariably his pictures have good composition, and sometimes they have really splendid composition.

Obviously many of Catlin's pictures are memory paintings of incidents freshly observed. His bison hunts, his groups of Indians in games, in fact all his scenes of active wild life, must have been painted on the spot, as soon as seen and in their natural environment, but they could only have been done from memory, as usually they represent many figures or animals, generally in violent motion. Evidently Catlin had a strong artistic memory and it was that quality which enabled him to get so much life in his work. For his humans and animals have both action and motion: they are alive, they stand plumb on their feet, they walk, they run, they jump: they have none of the arrested motion of certain academic work. His groups of figures render the movements of the groups; you feel the way each group is moving. Except in his portraits, his humans are never posing. There is no rigidity in his work. His one weak spot in regard to motion is that he painted some of his galloping horses and bison with the incorrect open-scissor action which no white race man ever discovered was wrong, until instantaneous photography obliterated it from art.

It is the matter and not the manner of Catlin's pictures, however, which is of supreme importance. The paramount value of his pictures lies in the subjects and in the fact that the subjects are handled realistically. His pictures are extremely original through their subjects and they are absolutely individual because the subjects appealed to Catlin and were motives to him. There is nothing idealistic about his pictures; they are not imaginative; they are pure realism. His Indians are not the Indians of romance nor of the warped mentality of hostile whites; his Indians are the real thing.

Catlin is a great illustrator-painter. He painted endless incidents of the life of the American natives realistically and accurately. He painted his pictures of the wild Indians while actually living among them, with the scenes which he was painting, the real history of the Indians, actually being enacted before him. And the result is that

Catlin, as no other artist, makes the Indians a part of their surroundings, a part of the wild life of the plains, of the forests, of nature; he makes them a living part of their environment. His pictures place before us the Indians in the chase, in the dance, in the tepee, in fact in all the incidents of life. He shows us in an unexcelled way how people who lived by hunting with stone weapons obtained their livelihood; and he makes it clear that killing bisons and grizzly bears was anything but child's play to a man armed with a stick tipped with a pointed stone.

Catlin looked at the Indians with a friendly eye. He lived with them for years, he admired them as models and as characters, indeed one might say that he loved them. The usual idea that the Indian is a lazy, good-for-nothing individual, who lets his squaw work and slave for him, is really a libel and is dispelled by Catlin. It is formed from the Indians on reservations, who received their beef and blankets from government agents. When the Indian was corralled and the bison exterminated, the Indian's occupation was gone. The real Indian provided meat and skins for his family; food and the materials for clothing and teepees. To obtain meat and skins from deer, bison and grizzlies with a flint-headed arrow was enough for any man; it took his time and strength. When he hunted day after day and week after week and year after year, in good and bad weather, in sunshine and sleet, in cold and heat, he considered and he considered rightly, that he was entitled to have his food and his clothing prepared for him at home. He did not go downtown to deal in finance, nor did he stand up in a store to sell millinery, but in his native conditions he was just as much a business man as any American of to-day, and just as much entitled to find a good dinner at home in the evening with his dress clothes laid out nicely brushed, as our hardest worked lawyer or physician.

It is a godsend for the history of the American Indians that Catlin was never taught to draw, that he lacked the opportunity of studying and learning to paint like everyone else. If he had been trained in the schools of the day, probably he would have developed the what might be termed rather grandiloquent style of some of the so-called Hudson river school. Fortunately he did not. For as a result of being self-taught and of living most of his life in the wilder-

ness, Catlin's painting is truly individual, it is unlike anyone else's, a sure test that he had real underlying art powers. His pictures are not founded on tradition and therefore perhaps have a certain primitive look; indeed Catlin more than any American might be called a primitive. The painters of to-day would not see things as Catlin did; they are too learned. And from the standpoint of modern art some phases of his work would be called bad, and yet it is probably accurate to say it is partly those very *naïvetés* which make it so good.

Catlin's position among artists is unique. He devoted his life, with almost no pecuniary reward, to delineating the deeds and the artistic beauties of a vanishing race. His pictures are the great record of our displaced predecessors. His incident pictures are painted directly on the spot, either from the Indians posing for him or from memory immediately afterwards. He painted hundreds of such incident pictures from occurrences he actually saw. No one else has done anything of the kind except most sporadically. No one could do it now. For all these scenes have disappeared from the face of the earth. Anyone in the future, artist or layman, who wants to see how our Indians, untouched by white civilization, actually lived and appeared, must turn to Catlin. In the coming centuries the Indians more and more will amalgamate and fuse with their conquerors and the more they do, the greater value will scientists attach to the wonderful records which Catlin has left of the copper-colored men who once ranged and roamed in wild and unrestrained liberty from Alaska to Tierra del Fuego.

PARASITISM AMONG THE RED ALGÆ.

By WILLIAM ALBERT SETCHELL.

(Read April 19, 1918)

The question as to when a particular plant is, or is not, a parasite is often difficult to answer, although in many cases the parasitic relation is readily to be inferred because of certain morphological peculiarities and also because of the apparent dependence of the one (parasite) upon another (host) in the matter of nourishment. The fundamental conception is, of course, that the parasite draws upon the host for materials of greater or less metabolic value, but, as to amount and extent, is difficult of demonstration and may be inferred largely from various indications of a morphological nature.

There are also to be considered in connection with parasites, especially among the thallophytes, epiphytes and endophytes. A true epiphyte uses the plant upon which it grows only for mechanical support. Its metabolism is independent of that of the plant on which it grows. It is conceivable that even those epiphytes which penetrate the tissues of the supporting plant do so only in a mechanical way, although it seems probable that penetration is usually associated with the establishment of metabolic relations.

In case of the endophyte, a variety of relations seems to exist between it and the plant it inhabits. Epiphytes exist both among cormophytes and thallophytes. Endophytes are always thallophytes and they may grow entirely within the body of another plant or only partially so. Some algal endophytes only penetrate between the layers of the outer walls while others descend deep among the cells of the plants they inhabit. It seems very possible that there may be parasitic relations between many, or most, of the endophytes and their "hosts."

Epiphytes are numerous among the red algæ and, while no exact enumeration has been made, it seems safe to say that, at least, half

of the known species are epiphytes. It is very desirable that these should be investigated as to their relations to the plants on which they grow. Where epiphytes are constantly observed on a single or even on a few closely related plants it is to be suspicioned, at least, that there may be some, even if slight, parasitic relation. *Polysiphonia fastigiata* (Roth) Grev., *e. g.*, is an epiphyte whose constant occurrence on *Ascophyllum nodosum* (L.) Le Jolis has been noticed. R. J. Harvey Gibson (1891, p. 132) states that "The attachment of the epiphyte to *Ascophyllum* is very intimate" and says farther that "root filaments given off from the base of the frond penetrate deeply into the tissue of the host and wander amongst the cortical cells and medullary hyphæ." A similar penetration of the "host" usually takes place from the base of *Pterosiphonia Woodii* (Harv.) Falkenb. into the tissues of the Laminariaceæ it grows upon, as observed by N. L. Gardner and myself. *Callithamnion Lejolissea* Farlow penetrates deeply into the tissues of the nodes of the *Amphiroa* on which it is always found. Clara K. Leavitt (1904, p. 294) describes the penetration of *Microcladia californica* Farlow and also of an unnamed species of *Callithamnion* into the fronds of "*Callymenia Phyllophora* J. Ag." The list will undoubtedly be considerably extended after carefully examining other "epiphytes." It remains a question as to whether such forms are to be considered as parasites or not. The *Polysiphonia* is of low stature, but can hardly be considered as reduced. The *Pterosiphonia* and *Microcladia* are often found in very much reduced forms but not as a rule, and they show little, if any, loss of color.

Certain forms of penetration of the plant upon which they exclusively are to be met with occur in the cases of *Placophora Bideri* J. Ag. and *Ceramium codicola* J. Ag. Both species grow on *Codium* and possess rhizoidal filaments which differ from any of the regular outer structures and which penetrate, at least, between the utricles of the *Codium*. This does not seem to indicate true parasitism.

Among the marine species of *Chantransia* (or *Acrochætium*) are some epiphytes which are confined to a single "host" and which are partially, at least, parasites (cf. Rosenvinge, 1909, p. 82). The plants of this genus are all small, whether growing on rock, or

as true superficial epiphytes, or as wholly or partially endophytes. Only one of these species has been observed to actually attack the cells of the host, and that is *Chantransia cytophaga* Rosenvinge, growing in the fronds of *Porphyra umbilicalis*. This species seems certainly to be reckoned among the parasites.

Of endophytes or endozoic species there are a few reds. Besides species of *Chantransia* or *Acrochatum* alluded to above, there are *Schmitziella endophlæa* Bornet & Batters and *Rhodochorton membranaceum* Magnus. These are simply within the outer membranes, the former of *Cladophora*, the latter of *Sertularia*, one of the Bryozoa. Somewhat more deeply, and also partially, endophytic is *Rhodochorton subimmersum* Setchell & Gardner, whose main filament is totally included and whose short, erect tetrasporangia-bearing branchlets are emersed at their tips. There are several similar endophytes to be found among the red algæ which may be slightly parasitic, but it is difficult to determine this with exactness.

In contrast with the various epiphytes and endophytes, such as those mentioned above, are those red algæ which seem undoubtedly to be parasites. In placing these among parasites, three criteria of probable parasitism have been considered, viz., penetration, reduction of thallus and loss of color. It has been considered that at least the first two ought to be present and in very evident form to constitute evidence of parasitism, while the last may or may not be noticeable.

The undoubted parasite enters the host plant, as a rule, by rhizoidal filaments, or more solid haustoria, which penetrate beyond the superficial assimilating cells into the conducting tissues. It usually also, establishes more or less conspicuous pit connections between its haustoria and the cells of the host.

The reduction of the thallus or vegetative plant body varies much in the different parasites. As mentioned above, some dwarfing takes place even in certain plants which it seems best to consider, for the time being, at least, as epiphytes, but in those usually reckoned as parasites, dwarfing is extreme and usually accompanied by a greater or less condensation of the thallus, resulting in tubercular growths of greater or less extent. Taken in connection with

penetration, extreme dwarfing or condensation of the thallus may be taken to indicate true parasitism of greater or less degree. At the same time the reproductive organs present little if any metamorphosis.

In color, parasites vary from little if any loss of pigment to cases where none is present. Loss of color is always associated with extreme penetration and very considerable dwarfing or condensation.

It is only within the last thirty years that the fact has been realized that there exists a group of peculiar and undoubted parasites among the red algæ, although a few cases were noted before that time. Probably the first reference to such a parasite is that by Lyngbye in noting that certain tubercles on "*Sphærococcus Brodiai*" (*Phyllophora Brodiai*) called by him "*Chatophora membranifolii*" and which had been considered to be the nemathecium of the plant on which they were found, were no part of the "*Sphærococcus*" but belonged to a parasite. This was in 1819 (p. 11, pl. 3, f. B, 3, 4). In 1834 Lyngbye describes this plant in more detail, naming it *Chatophora subcutanea* (1834, pl. 2135), but saying nothing definitely as to its being parasitic. Kuetzing, in 1843 (p. 177, pl. 45, f. IV), re-described and named it *Actinococcus roseus*, seemingly unaware of the earlier description of Lyngbye. The species, which now bears the name *Actinococcus subcutaneus* (Lyngb.) Rosenvinge, later became the object of a considerable discussion and difference of opinion as to its exact nature (cf. Schmitz, 1893, etc.). It is now recognized as a true parasite by most phycologists.

The second parasite belonging to the red algæ to be recognized was *Ricardia Montagnei* described by Derbes and Solier in 1856 (p. 209, pl. 1). This plant, usually assigned to the Bonnemaisoniaceæ, forms ovoid red bladders of larger or smaller size, on the tips of species of *Laurencia*. Its basal portion occupies the apical pit of the branches of the *Laurencia* and penetrates into its tissue (cf. Oltmanns, 1905, p. 326, f. 580).

In 1874-75, Reinsch published his "Contributiones ad Algologiam and Fungologiam" and in this he described a number of tubercles found on various red algæ which he believed to be parasitic members of the same group. Among the tubercles thus described by Reinsch, some are undoubtedly simply warts or pathologic out-

growths of the plants on which they are found, but some are undoubtedly parasites. Such are some of the plants belonging to his genera *Choreocolax* and *Syringocolax*, but Reinsch did not find any cystocarps or other organs of frutification on any of his specimens.

The work of Reinsch produced little immediate effect and the basis of truth in it was not recognized until some years had passed. In 1877, however, there appeared the first convincing description and illustration of a parasitic red alga. In this year, Solms Laubach published his paper on *Janczewskia verruciformis* which possessed all the characteristics convincing of parasitism, viz., deep penetration of the host plant (*Laurencia obtusa*), reduction of the thallus to a tubercle and color varying from dark red, through orange to pale yellow. In addition to these, it showed cystocarps, antheridia and tetrasporangia. In the case of *Janczewskia*, as described by Solms, there can be no doubt either as to the parasitism or as to the nature of the parasite. It is to be noted here also, that the parasite is very closely related to its host and is the first of this sort of parasite to be described among the red algæ.

Between the years 1876 and 1889, little was done to further our knowledge of parasitism among the red algæ. McNab (1876) recorded the finding of *Choreocolax polysiphoniæ* Reinsch near Dublin and speaks of its tubercular thallus and penetrating rhizoidal portion, but mentions no reproductive organs of any kind. Bornet, in 1878 (pp. 97-99, pl. 50, f. 1-8) described on *Jania rubens* Lamour a very distinct parasite which he named *Melobesia Thureti*, noting that it had been described by Harvey as early as 1849 (pl. 201) as a second kind of tetrasporangial conceptacle of *Corallina squamata* Park. In 1881, Solms Laubach (p. 57, pl. 1, f. 5, pl. 3, f. 12) described a second parasitic *Corallina* which he named *Melobesia deformans* growing on and in *Jania natalensis* Harv. and whose apices it distorts through the action of its penetrating rhizoidal filaments. Moebius, also, described a Ceramiaceous parasite on *Centroceras clavulatum* (Roth.) J. Ag. in 1885 (pp. 77-80, pl. 7), which he named *Episporium centroceratis*.

The year 1889 may be considered to be the real starting point in the genuine study of the parasitic red algæ. Farlow (1889, p. 6) made known the tetrasporangia of *Choreocolax Polysiphoniæ*

Reinsch. Schmitz and Reinke (cf. Reinke, 1889, p. 28) described *Harveyella mirabilis* (Reinsch) Schmitz et Reinke (*Choreocolax mirabilis* Reinsch) with its antheridia and cystocarps, and finally Schmitz, in his "Systematische Uebersicht der bisher bekannten Gattungen der Florideen," enumerated eight distinct genera of parasitic red algæ, viz., *Actinococcus* Kuetzing, *Ricardia* Derbes et Solier, *Choreocolax* and *Syringocolax* Reinsch, *Janczewskia* Solms, *Epi-sporium* Moebius, *Harveyella* Schmitz et Reinke and *Choreonema* Schmitz. The last genus was created to contain the *Melobesia Thureti* Bornet.

The enumeration of Schmitz, together with the discovery of tetrasporangia, antheridia and cystocarps in *Janczewskia* and in *Epi-sporium*, the antheridia and cystocarps in *Harveyella*, the cystocarps and tetrasporangia in *Choreonema*, and the tetrasporangia in *Choreocolax* were convincing as to the existence of real parasites and led to search for more. In 1891, Richards described the cystocarps as well as the tetrasporangia of *Choreocolax Polysiphoniæ* Reinsch. In 1892 Batters made known *Gonimophyllum Buffhami* with its cystocarps and tetrasporangia. In 1892, Schmitz published a discussion of the tubercular growths on various red algæ, with a view to distinguishing those which are true parasites from those which are merely warts or galls. In 1893 Heydrich created the genus *Pleurostichidium*, a Rhodomelaceous genus parasitic on one of the Fucaceæ (*Fucodium*) in New Zealand. It is dwarf, penetrating and provided with antheridia, cystocarps and tetrasporangia. In the same year, Schmitz published his very memorable paper on *Actinococcus*. After a full discussion, Schmitz distinguished between *Actinococcus* and the true nemathecium of *Phyllophora* and enumerated four species of *Actinococcus* besides two for *Colacolepis* and two for *Sterrocolax*. He also considered the placing of these genera, deciding upon the Gigartinaceæ, the same family to which the hosts belong, rather than the Squamariaceæ, where *Actinococcus* had previously been assigned by J. G. Agardh.

The *Actinococcus* paper of Schmitz provoked considerable discussion. Darbishire (1894) who had been investigating the species of *Phyllophora* very carefully, held that the so-called *Actinococcus* species were the true nemathecium of *Phyllophora* and repeated this in

1895. Later, in 1899, however, Darbishire, after the death of Schmitz in 1894, published the results of further investigation which resulted in finding the germinating stages of *Actinococcus* in the antheridial cavities of the *Phyllophora* and came to the same point of view as Schmitz. This point of view was also confirmed by the investigations of Gomont (1894).

In 1894 Kuckuck described the tetrasporangial plant of *Harveyella mirabilis* (Reinsch) Schmitz et Reinke, under the name of *Choreocolax albus*, and in 1895 Batters published the genus *Callocolax* of Schmitz, a genus whose single species is parasitic on *Callophyllis*, which is very closely related to itself.

In 1896-97 appeared those parts of Engler and Prantl's "Natuerlichen Pflanzenfamilien" dealing with the red algæ and with whose preparation Schmitz had long been busy. The genera of parasitic red algæ were worked over either by Schmitz himself, or by Hauptfleisch or, in case of the Rhodomelaceæ, by either Schmitz or Falkenberg. The total number of genera of parasitic red algæ was increased from the eight detailed in 1889 to nineteen, the five genera proposed as new in this work belonging entirely to the Rhodomelaceæ and parasitic on other members of the same family.

Since 1897, additions have been made to the list of both genera and species of parasitic red algæ. One genus already proposed, viz., *Callocolax*, was not included in the Engler and Prantl account. This makes twenty genera known up to the close of 1897. Rosenvinge added *Ceratocolax* in 1898 (p. 34) and in the same year Foslie (1898, p. 7) created the genus *Chatolithon* to receive the *Melobesia deformans* Solms. Falkenberg (1901) in his monograph of the Rhodomelaceæ, published more detailed descriptions and figures of the various parasitic genera of this family previously proposed by Schmitz and by himself, but added no new genera. In 1905, Setchell and Lawson (cf. Setchell, 1905, p. 7) proposed the genus *Peyssonneliopsis* and in 1910 Setchell and Wilson) cf. Wilson, 1910, p. 81) proposed the genus *Gracilariophila*, which from their point of view is a *Gracilaria*-like genus parasitic on a *Gracilaria* (cf. however Eddelbüttel, 1910, p. 230, 231, and Svedelius, 1911, p. 220—). In 1913, Yendo (p. 283) described and figured a most interesting

new genus of parasitic red algæ belonging to the Rhodomelaceæ, which he named *Benzaitenia*. The single species is parasitic on other Rhodomelaceæ. Finally, M. A. Howe (1914, p. 90) has made known the genus *Lobocolax*, which he refers doubtfully to the "Nemalionaceæ" (Helminthocladiaceæ Auctt.). The single species forms tubercles on *Prionitis decipiens* (Mont.) J. Ag.

To summarize the genera thus far proposed of parasitic red algæ, there were nineteen recorded by Schmitz and Falkenberg in 1897, and six have been proposed since that time. In addition, it may be stated that there are four additional genera as yet undescribed in the collections of the writer. The total number of genera known to the writer, therefore, amounts to twenty-nine. These are all reduced or condensed as to the thallus, penetrating and apparently forming protoplasmic connections with the host plants and varying from full deep red to pure shining white.

In regard to species, the number assigned thus far to these genera and fairly certain, number about fifty and it seems best to give a list of these arranged by families and to indicate in connection with each its host or hosts, in order that the basis for further discussion may be made clear. In this list there have been included only those species which seem fairly certain as representing definite and distinct parasites. All decidedly doubtful species are omitted. An * is placed against those species which are credited to hosts among the red algæ but not of the same family as the parasite and a † against those parasitic on Phæophyceæ. The rest are parasitic on red algæ of the same family as themselves.

HELMINTHOCADIACEÆ.

- *1. *Lobocolax deformans* Howe (1914), on *Prionitis decipiens* Mont. J. Ag.

GELIDIACEÆ.

- *2. *Choreocolax polysiphoniæ* Reinsch (1874-75), on *Polysiphonia fastigiata* (Roth) Grev.
 *3. *Choreocolax tumidus* Reinsch (1874-75), on *Ceramium* and *Cystoclonium purpuracens* (Huds.) Kuetz.
 *4. *Choreocolax cystoclonii* Kylin (1907), on *Cystoclonium purpurascens* (Huds.) Kuetz.

- *5. *Harveyella mirabilis* (Reinsch) Schmitz et Reinke (1889), on *Rhodomela*.
- *6. *Harveyella pachyderma* (Reinsch) Batters (1902), on *Gracilaria confervoides* (L.) Grev.

GIGARTINACEÆ.

- 7. *Actinococcus subcutaneus* (Lyngb.) Rosenvinge (1893), on *Phyllophora Brodiaei* (Turn.) J. Ag. and *P. interrupta* (Grev.) J. Ag.
- 8. *Actinococcus aggregatus* Schmitz (1893), on *Gymnogongrus Griffithsia* (Turn.) Mart.
- 9. *Actinococcus peltiformis* Schmitz (1893) on *Gymnogongrus norvegicus* (Gunn.) J. Ag. and *G. crenulatus* (Turn.) J. Ag.
- 10. *Actinococcus latior* Schmitz (1893), on *Gymnogongrus dilatatus* (Turn.) J. Ag.
- 11. *Actinococcus mollis* M. A. Howe (1914), on *Gymnogongrus disciplinalis* (Turn.) J. Ag.
- 12. *Actinococcus Chiton* M. A. Howe (1914), on *Gymnogongrus linearis* (Turn.) J. Ag.
- 13. *Colacolepis decipiens* Schmitz (1893), on *Phyllophora Heredia* (Clem.) J. Ag.
- 14. *Colacolepis incrustans* Schmitz (1893), on *Phyllophora nervosa* (DC.) Grev.
- 15. *Sterrocolax decipiens* Schmitz (1893), on *Ahnfeldtia plicata* (Huds.) Fr.
- 16. *Sterrocolax crassior* Schmitz (1893) on "*Gymnogongrus fastigiatus* var. *crassior* Ruprecht."
- 17. *Ceratocolax Hartzii* Rosenvinge (1898), on *Phyllophora interrupta* (Grev.) J. Ag.
- 18. *Callocolax neglectus* Schmitz (1894), on *Callophyllis laciniata* (Huds.) Kuetz.

SPHÆROCOCCACEÆ.

- 19. *Gracilariophila oryzoides* Setchell et Wilson (1910), on *Gracilaria confervoides* (L.) Grev.

DELESSERIACEÆ.

20. *Gonimophyllum Buffhami* Batters (1892), on *Nitophyllum laceratum* (Gmel.) Grev.

BONNEMAISONIACEÆ.

21. *Ricardia Montagnei* Derbes et Solier (1856) on *Laurencia obtusa* (Huds.) Lamour.
 22. *Ricardia Montagnei* var. *gigantea* Farlow, on *Laurencia* sp.

RHODOMELACEÆ.

23. *Janczewskia verrucæformis* Solms (1876), on *Laurencia obtusa* (Huds.) Lamour.
 24. *Janczewskia tasmanica* Falkenb. (1897), on *Laurencia Forsteri* (Mert.) Grev.
 25. *Janczewskia moriformis* Setchell (1914), on *Chondria atropurpurea* Harv.
 26. *Janczewskia lappacea* Setchell (1914), on *Chondria nidifica* Harv.
 27. *Janczewskia Gardnerii* Setchell et Guernsey (1914) on *Laurencia spectabilis* R. & R.
 28. *Janczewskia Solmsii* Setchell et Guernsey (1914), on *Laurencia subopposita* (J. Ag.) Setchell.
 29. *Microcolax botryocarpa* (Hook. et Harv.) Schmitz (1897), on *Strebdocladia neglecta* Schmitz.
 †30. *Pleurostichidium Falkenbergii* Heydrich (1893), on *Xiphophora chondrophylla* (R. Br.) Harv.
 31. *Colaconema pulvinatum* Schmitz (1897), on *Vidalia serrata* (Suhr.) J. Ag.
 32. *Colacodasya inconspicua* Schmitz (1897), on *Polysiphonia* and *Heterosiphonia*.
 33. *Colacodasya verrucæformis* Setchell et McFadden (1911) on *Chondria*.
 †34. *Haplodasya Reinboldii* Falkenberg (1897), on *Cystophora retroflexa* (Labill.) J. Ag.
 35. *Stromatocarpus parasiticus* Falkenberg (1897), on *Polysiphonia virgata* (Ag.) Spr.

36. *Tylocolax microcarpus* Schmitz (1897), on *Lenormandia spectabilis* Sond.
37. *Benzaitenia yenoshimensis* Yendo (1913), on *Chondria crassicaulis* Harv. and *Laurencia paniculata* J. Ag.

CERAMIACEÆ.

- *38. *Syringocolax macroblepharis* Reinsch. (1874, 75) on *Gelidium cartilagineum* (L.) Gaill.
39. *Episporium centroceratis* Moebius (1885), on *Centroceras clavulatum* Mont.

SQUAMARIACEÆ.

- *40. *Peyssonneliopsis epiphytica* Setchell et Lawson (1905) on "*Meredithia californica* J. Ag."

CORALLINACEÆ.

41. *Choreonema Thureti* (Bornet) Schmitz (1889), on *Jania rubens* Lamour and *Corallina squamata* E. & S.
42. *Chetolithon deformans* (Solms) Foslie (1898), on *Jania natalensis* Harv.

In addition to the species listed above and which have been selected from the species published as being certain or very nearly so, there have resulted from collections, chiefly by N. L. Gardner, on the Pacific coast of North America, some nine additional but as yet unpublished species, together with four additional genera, also as yet unpublished, as noted previously. All of these species are parasitic on genera closely related to themselves. To make this more evident and, at the same time, to make known the distribution among the families of red algæ of the new genera and species, a brief resumé of these as yet unpublished species is appended. In Sphærococcaceæ, a new species of *Gracilariophila* has been found on *Gracilaria Cunninghamii* J. Ag.; in Rhodymeniaceæ, three new genera of a single species each on *Faucheia laciniata* J. Ag., *Rhodymenia Palmetta* (Esp.) Grev.?, and on *Plocamium coccineum* (Huds.) Lyngb., respectively; in Delesseriaceæ, two new species of *Gonimophyllum*, one on *Nitophyllum Ruprechtianum* J. Ag. and an-

other on a species of *Delesseria*, as well as a single species of a new genus on *Neuroglossum Andersonianum* J. Ag.; and in Rhodomelaceæ, two new species of *Stromatocarpus* on *Pterosiphonia Baileyi* (Harv.) Falkenb. and on another species of the same genus respectively. These new genera and species are in a fairly advanced stage of preparation towards description and illustration.

In summarizing the distribution of these distinctive parasitic genera, among the red algæ, we find the results as follows:

Helminthocladiaceæ	1 genus with 1 species.
Gelidiaceæ	2 genera with 5 species.
Gigartinaceæ	5 genera with 12 species.
Sphærococcaceæ	1 genus with 2 species.
Rhodymeniaceæ	3 genera with 3 species.
Delesseriaceæ	2 genera with 4 species.
Bonnemaisoniaceæ	1 genus with 2? species.
Rhodomelaceæ	9 genera with 17 species.
Ceramaceæ	2 genera with 2 species.
Squamariaceæ	1 genus with 1 species.
Corallinaceæ	2 genera with 2 species.

This summary shows clearly the extent of the distribution of parasitic genera and species through the group of the red algæ and the fact that they are, thus far, known only from eleven of the twenty-one families into which the group is usually divided. It also shows that of these eleven families, two, viz., Gigartinaceæ (with 5 genera and 12 species) and Rhodomelaceæ (with 9 genera and 17 species) contain one half or over of the known genera and species.

Besides the literature dealing with the strictly systematic side and describing, for the most part new species, there are a few papers which attend mostly to other matters connected with the parasitic red algæ. Such, for instance, is the paper by Nott (1897) discussing the finding of certain parasitic red algæ on the coast of California, and a similar paper by the writer published later (cf. Setchell, 1905). Sturch (1899) published the results of a careful study into the structure, development, and nature of the parasitism of *Harveyella mirabilis* Schmitz and Reinke and its systematic position. In 1905, Oltmanns (p. 319 et seq.) discussed parasites among the algæ,

particularly describing and illustrating the parasitism of *Ricardia*, *Actinococcus*, *Harveyella*, *Janczewskia*, *Stromatocarpus*, *Choreonema* (" *Melobesia Thureti* Born.") and *Chætolithon* (" *Melobesia deformans* Solms"). The penetration, reduction of the thallus and natural relationship to the host plant are all dealt with. This is the only general discussion of the parasitism of the red algæ thus far published. In 1910 Eddelbüttel published a general account of parasitism among the red algæ, with special reference, however, to *Choreocolax* and *Harveyella*. This account dealt particularly with the systematic position of *Choreocolax* and *Harveyella*, advocating removing them from the Gelidiaceæ, where they had been placed by Schmitz, and placing them among the Gigartinales, as Sturch (1899, p. 98) had advocated. He also discussed *Gracilariophila* Setchell and Wilson (1910), suggesting placing it near, if not uniting it with, *Choreocolax*. I am unable to agree with this latter view because of the very different structure of the cystocarp in the two genera, the essentials of which, viz., the different shape and arrangement of the spores, Eddelbüttel did not mention or seem to consider in his discussion.

From all the previous consideration, two things, at least, seem plain. First, there are approximately twenty-nine genera and fifty-one species of undoubted and peculiar parasites among the red algæ. Doubtless there are many of similar character to be discovered. In fact, there is knowledge, but of unsatisfactory character, of the existence of a number of such. Doubtless also, there are some, possibly many, at least partial parasites among the various "epiphytes" and "endophytes," so numerous in the group.

Second, there is an overwhelming restriction in the matter of parasitism on other red algæ and even on other members of the same family. Of 51 parasites enumerated above, 41 are fairly certainly parasitic on another member of the same family. This is a little over 80 per cent. of the whole number. Of the remainder, 8 or a little less than 16 per cent. are parasitic on red algæ not of the same family (*i. e.*, practically 96 per cent., therefore, parasitic on other red algæ), while only two or a little less than 4 per cent. are parasitic on algæ (brown) other than red.

Although acquainted with a far less number of cases Batters

(1892, p. 66 and 1895, p. 317), Schmitz (1893, p. 390) and Oltmanns (1905, p. 334) have all spoken emphatically of the fact that so many of the parasitic red algæ are restricted to near relatives as hosts. Oltmanns further remarks (loc. cit.) that no satisfactory explanation of this can be brought forward. The suspicion has been produced, especially earlier in the progress of our knowledge, that some of these parasites, especially some species of *Actinococcus*, are really parasitic tetrasporangial generations of the hosts they inhabit. Darbishire (1899, p. 264) has voiced this suspicion and has stated his opinion that while this is not impossible, it is not very probable. The probability, as it seems to the writer, is, however, that the various parasites, or some of them, may have originated in close connection with their hosts by some mutation decreasing the chlorophyll content or power in one or other of the different forms of spore. Such an inducement to increase the power of penetration and possible protoplasmic connection between a spore (tetraspore or carpospore) germinating in position might, it would seem probable, initiate parasitism on the parent plant, and this parasitic tendency increasing penetration and dwarfing, might, therefore, be inheritable.

There is one case known which seems to be such a case or in line with such action. This is the condition found in *Agardhiella tenera* (J. Ag.) Schmitz ("*Rhabdonia tenera*" J. Ag.) by Osterhout (1896). It was noticed that the tetrasporangial plants have, in many cases, numerous short bristle-like branches or proliferations projecting at right angles to the main stem and branches, but that the antheridial and cystocarpic plants are always destitute of them. Examination showed that these peculiar branchlets are usually antheridial, while full-sized antheridial plants are rare. Sometimes, however, the bristly short branchlets have tetrasporangia or cystocarps and the three kinds of reproductive bodies are sometimes borne on branchlets side by side. Some of the branchlets remain sterile "but in the majority of cases they bear reproductive organs before they are more than a quarter of an inch in length." (Osterhout, loc. cit., p. 420.)

It was found by Osterhout that the zonate tetrasporangia divide in regular fashion forming what seem to be four tetraspores each, arranged serially. These spores then sometimes divide further by

oblique divisions and as this continues the contents of a tetrasporangium act as a whole, producing penetrating rhizoidal filaments below and a regular, though much dwarfed, *Agardhiella*-frond above. The rhizoidal filaments penetrate even into the region of the medullary hyphæ of the parent plant and establish "secondary connections" with them. There seems certainly to be here a parasitic red alga in the making. There exist full-sized plants of *Agardhiella tenera* of all three sorts, viz., antheridial, cystocarpic and tetrasporangial. There exist also dwarf plants, parasitic on, but arising from, the tetrasporangial plant. While these dwarf plants, and they are very much reduced and simple, are largely antheridial, yet, according to Osterhout, all three kinds of dwarf plants, viz., antheridial, cystocarpic and tetrasporangial, may exist side by side, all parasitic on and probably arising from the same full-sized tetrasporangial plant. In order that our knowledge of this interesting and seemingly very significant case may be more complete, it is very desirable that culture be made from the spores (both carpospores and tetraspores, if obtainable) of the dwarf plants. It is very desirable that this be undertaken by some investigator who has access to abundant growths of these plants. The very similar species, *Agardhiella Coulteri* (Harv.) Setchell, of the California coast has not been observed to produce dwarf plants (or bristly proliferations) from the tetrasporangial generation.

In summarizing, then, the aim of this paper, it may be said to be intended to indicate how general is the extent of the parasitism of the parasitic genera and species of red algæ upon their near relatives and to draw attention to the similarity of these cases and the case of the production of a dwarf parasitic generation from the tetrasporangia of *Agardhiella tenera* and with the hope of suggesting the probability of their origin.

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A STUDY OF SOME ANT LARVÆ, WITH A CONSIDERATION OF THE ORIGIN AND MEANING OF THE SOCIAL HABIT AMONG INSECTS.¹

By WILLIAM MORTON WHEELER.

(Read April 19, 1918.)

The care lavished by ants on their brood is a matter of such frequent and easy observation that it has always excited wonder and comment. When a colony is disturbed at the height of the breeding season the brood is at once seized and carried to a place of safety, and when more closely observed in artificial nests the behavior of the workers is seen to be very largely a constant round of the four different activities of feeding, licking, transporting and defending the young. Swammerdam says in that wonderful volume, the "*Biblia Naturæ*" (1737-1738): "Incredible *στοργή* et cura Formicæ educant summamque dant operam, ne vel tantillum quod spectet eorum Vermiculorum educationem atque nutritionem omittant"—"with incredible affection and care the ants bring up their vermicules and omit not the least thing appertaining to their education and nurture." He intentionally uses the word *στοργή*, from the verb *στέργειν*, to express his belief that love or affection impels the ant to care for her young, since there is no Latin equivalent for a term which to the Greek meant the affection of the members of a human family for one another as distinguished from other forms of "tender feeling."² And observers since Swammerdam seem uniformly to have agreed with him, though more modern writers often use such terms as "care of the brood" as more suited to the present colorless and noncommittal stage of natural history.

Now it must be conceded that Swammerdam's statement calls

¹ Contributions from the Entomological Laboratory of the Bussey Institution, Harvard University. No. 147.

² Plato in the "Laws," 754B, uses the verb in its typical Greek sense when he says: *καὶς στέργει τε καὶ στέργεται ὑπὸ τῶν γεννησάντων*.

attention to a real problem, but one that belongs to the psychologist and not to the biologist. I am quite willing to admit that there may be in ants some feeble analogue of the parental feelings of man and the highest animals, but as a biologist I am bound to seek and if possible to find some ethological or physiological basis for the ant's behavior toward her brood. Like other students of insects I have, no doubt, often taken too much for granted and have unquestionably committed the eighth deadly sin, called by the orthodox behaviorists "anthropomorphism," not once but many times. By way of partial penance I offer the following paper.

I confess that I took the Swammerdamian conception for granted till recently, while studying a collection of ants made in the Belgian Congo for the American Museum of Natural History by my friend Mr. H. O. Lang, I came upon some facts which seem to throw a flood of light on the true meaning of the relations of ants to their brood. These relations now appear to me so simple and unequivocal that I find difficulty in understanding how they could have remained so long unperceived, especially as a host of other facts had been insistently pointing in the same direction. Our blindness seems to have been due to regarding the adult ants as the only active factors in the brood relationship. We supposed that the larvæ, probably because they are such sluggish, legless maggots, were merely the inert and passive objects of the feeding, licking, transportation and protection. One result of this assumption has been a general neglect of the study of larval ants. Even their morphology has received little attention. There are a few valuable papers by Berlese (1901), Karawaiew (1896) and Pérez (1902) on the metamorphosis of ants, a single paper by Emery (1899) devoted to the external characters of the larvæ in a selected series of species and a number of scattered descriptions and figures, published mainly for taxonomic purposes, by myself and others.

I regret that in the past I failed to study the larval ants more closely and more continuously, especially as the meaning of some of the unpublished records in my notebooks of 1899 and 1900 is clear to me only now after the lapse of nearly twenty years. When I took up my work at the University of Texas in the fall of 1899 as a morphologist accustomed to well-furnished northern and European

embryological and anatomical laboratories and libraries, I found so little apparatus for the work in which I had been trained, that I fell into a peculiar listlessness and was for some weeks unable to concentrate my attention on any subject that seemed worthy of investigation. One day, while I sat on the bank of Barton Creek, near Austin, in the very spot where, as I later learned, MacCook had worked on the famous agricultural ant (*Pogonomyrmex molefaciens*), I happened to see a file of cutting ants (*Atta texana*), each with its piece of leaf poised in its mandibles. I vividly remember the thrill of delightful fascination with which I watched the red-brown creatures trudging along under their green loads, and it seemed to me that I had at last found a group of organisms that would repay no end of study. At that time there was no active myrmecologist in the country. MacCook had completed his work and Pergande was no longer deeply interested in the ants. Prof. Emery, however, and later Prof. Forel extended helping hands to me and forthwith sent me their numerous and important publications, and several of my students, notably C. T. Brues, A. L. Melander, C. G. Hartman and W. A. Long, never wearied of accompanying me on long excursions into the dry, sunny woods and canyons about Austin.

For a time I was greatly interested in the habits of three large ants of the primitive subfamily Ponerinæ, *Odontomachus clarus*, *Pachycondyla montezumæ* and *Lobopelta elongata*, which are common in Central Texas. I was able to show that their peculiar tuberculate larvæ are not fed with regurgitated food, like the larvæ of more specialized ants, but with pieces of insects (1900). Concerning the feeding of the *Odontomachus* larva I published the following remark (p. 24) :

These larvæ are placed by the ants on their broad backs, and their heads and necks are folded over onto the concave ventral surface, which serves as a table or trough on which the food is placed by the workers.

An unpublished note, the significance of which I did not appreciate at the time, refers to *Pachycondyla* and was recorded while I was studying the behavior of its extraordinary Phorid commensal, *Metopina pachycondylæ* (1901). It runs as follows:

As soon as the fragments of insects are placed on the larva's trough-like ventral surface, the latter is sometimes inundated with a copious, colorless liquid, which is at once eagerly lapped up by the attendant nurse.

I should now describe this behavior in the following words: As soon as the fragments are placed on its ventral surface, the larva discharges from its salivary glands a supply of secretion which is sometimes very abundant. This secretion, by means of a strong proteolytic ferment which it contains, digests the food extraintestinally and thus enables the larva to swallow and assimilate it, and at the same time serves in part as an agreeable draught for the nurse. The strong mandibles of the Ponerine larvæ are used for comminuting the insect food and thus preparing it for the action of the saliva. The larval feeding habits of our small northern species of *Ponera* and *Stigmatomma* are essentially the same as those of the Texan genera, as I showed in a special paper (1900a).

Within recent years I have examined the larvæ of a number of different Ponerinæ and have found them all to possess well-developed mandibles. All, in my opinion, except, perhaps, during their very youngest stages, are fed with fragments of insects, supplied directly by their nurses. In some species, the insect prey is probably given to the larva without previous dismemberment. I here describe and figure the young of three genera, *Myrmecia*, *Megaponera* and *Bothroponera*, as they differ considerably from one another and from all previously described Ponerine genera and will serve therefore to illustrate the diversity of larval structure within the subfamily.

Fig. 1 is from a photograph of the adult larva of *Myrmecia sanguinea*, one of the larger Australian bulldog ants, the most primitive of existing Formicidæ. It is milk-white, has the form of a vegetable marrow, with all the segments distinct, except those at the extreme posterior end of the body, the anterior segments are very slender and curved and the head is very small. The body is rather uniformly clothed with short, rapidly tapering, bristle-like hairs. Under a higher magnification the head (Fig. 2) is seen to have a projecting bilobed clypeus (*c*), broad, heavily chitinized, coarsely tridentate mandibles (*m*) and well-developed maxillæ (*x*) and labium (*l*), the former with two pairs of strongly chitinized peg-

shaped sensillæ (s'), the latter terminating in a broadly elliptical chitinous plate, with a single pair of knob-shaped sensillæ (s'') and the opening of the salivary duct (d) near the middle of its anterior border. The upper surface of the short, rounded cranium bears a

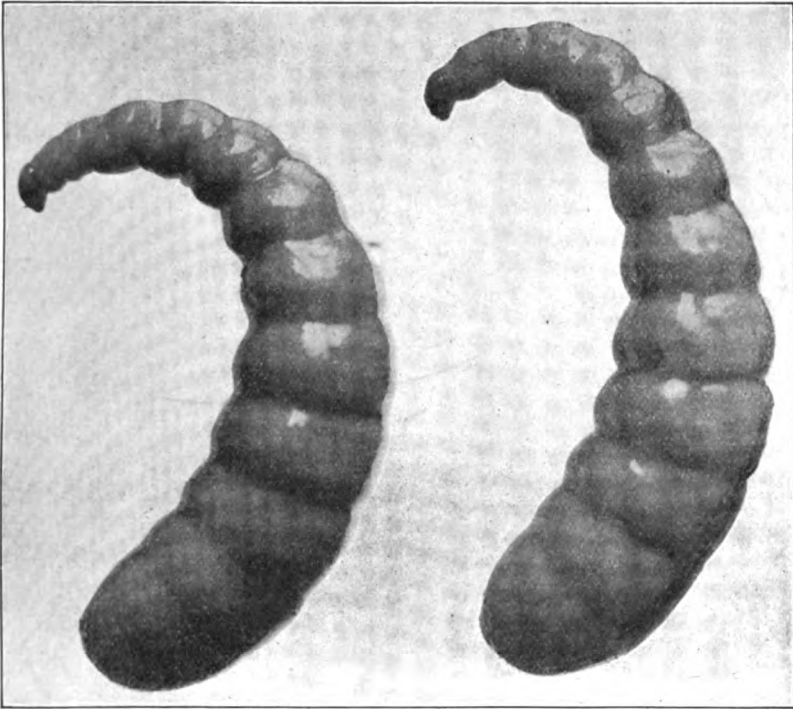


FIG. 1. Adult larvæ of *Myrmecia sanguinea* Fabr.

pair of minute antennal rudiments (n). When I collected this larva in New South Wales I was unable to learn anything of its feeding habits. Indeed, he who would make such observations would have to don a suit of armor specially designed to ward off the stings of this powerful and ferocious ant or be able to keep it in a large artificial nest. As I was continually travelling about I was unable to resort to the latter alternative. It is, however, not improbable that the *Myrmecia* larva is fed on whole insects, since the small head and very long mobile neck are very much as in certain solitary wasp larvæ (e. g., *Sphecius*), which gnaw a small hole in their prey and

then reach into its body cavity and devour its soft parts. The mandibles of the *Myrmecia* larva certainly show that it feeds on insect food.

The second larva (Fig. 3) is that of the "Matabele ant," *Megaponera fœtens*, of which Mr. Lang secured many specimens in the Belgian Congo. Arnold (1914) and others have shown that this

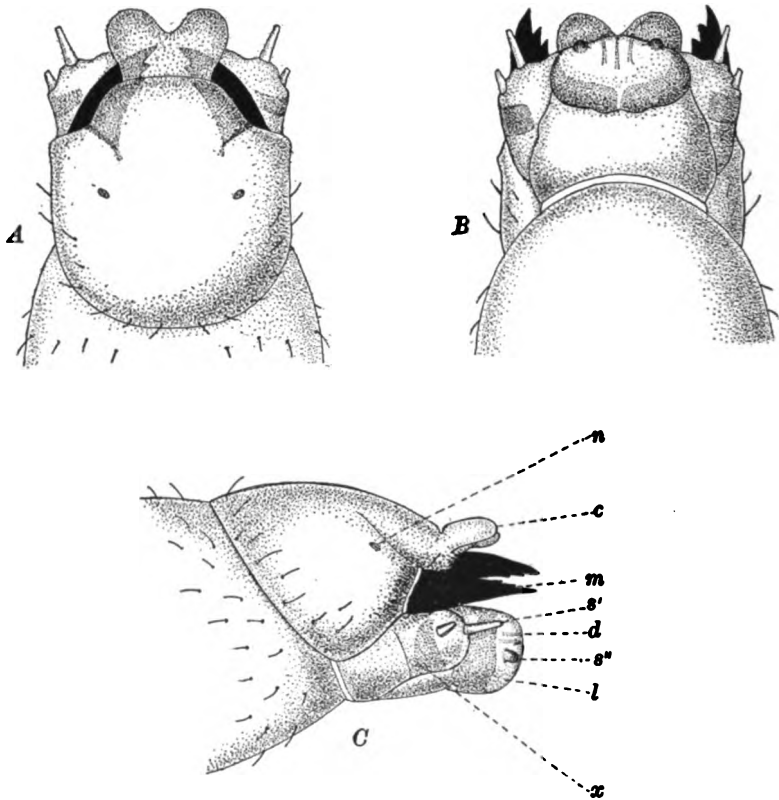


FIG. 2. Head of *Myrmecia sanguinea* larva. A, dorsal; B, ventral; C, lateral view; n, antenna; c, clypeus; m, mandible; x, maxilla; s, maxillary sensilla; l, labium; s', labial sensilla; d, opening of salivary duct.

ant preys on termites, the bodies of which it carries home agglutinated in the form of pellets (Alluaud in Santschi, 1914). It is very restless and changes its nesting site frequently, so that it is obliged to carry its young about a great deal and for considerable distances.

The larva is cylindrical, covered with a very tough, opaque, grayish, hairless skin and furnished with long, falcate mandibles. The pupa is enclosed in a very tough, black cocoon. These peculiarities are evidently adaptations to exposure to the air and light, to the exigencies of frequent and protracted transportation and to feeding on the bodies of termites brought into the nest by the workers. Mr. Lang actually observed the exposure of the black cocoons to the sunlight, a peculiarity of behavior which I had also observed in certain Australian Ponerinæ of the genera *Diacamma* and *Rhytidoponera* (1915).

The third larva (Fig. 4), that of *Bothroponera sublaevis*, one of four species of the genus, which I collected in Australia, has a very broad elliptical body, with a short, stout neck, strongly folded over onto the ventral surface, which is somewhat concave. The integument is also hairless and of a peculiar opaque, gray color. The sides of the three thoracic segments and first abdominal segment are furnished with fleshy tubercles and the mouthparts are very highly developed. It is placed on its back by the nurses and fed with fragments of insects deposited on its trough-like ventral surface as in our North American Ponerinæ.³

The feeding of the larvæ with pieces of insect food is not, however, confined to the Ponerinæ. Miss Fielde and I have shown that one of the commonest Myrmicine ants of the North Eastern States, *Aphanogaster fulva*, has the same habit. During late June, at the height of the breeding season, it is hardly possible to remove the stone covering a nest of this ant without finding one or more larvæ lying on their backs or sides in the act of feeding on the legs of flies or fragments of other small insects. Janet has observed simi-

³ Mayr described *Bothroponera* as a genus, but Emery, Forel and Santschi have been treating it as a subgenus of *Pachycondyla*. I return to Mayr's conception, because the adult, at least, of the Australian species of *Bothroponera* exhibits several peculiarities of behavior, such as the extrusion when captured of a mass of frothy bubbles from the tip of the gaster, and because of the structure of the larva, which is very different from that of *Pachycondyla* as will be seen by comparing Fig. 4 with my previously published figures of *P. montezumæ*. The larvæ of *Diacamma*, *Leptogenys* and *Odontomachus* bear a greater resemblance to those of *Pachycondyla*. *Bothroponera* is, moreover, confined to tropical Africa, Asia and Australia, whereas *Pachycondyla* is neotropical.

lar behavior in *Tetramorium cæspitum* and in some Camponotine ants of the genus *Lasius*. Hungry larvæ of *Aphanogaster* will even attack and devour smaller larvæ of their own species that lie within reach of their sharp mandibles.

Still the very young larvæ of *Aphanogaster* and possibly also

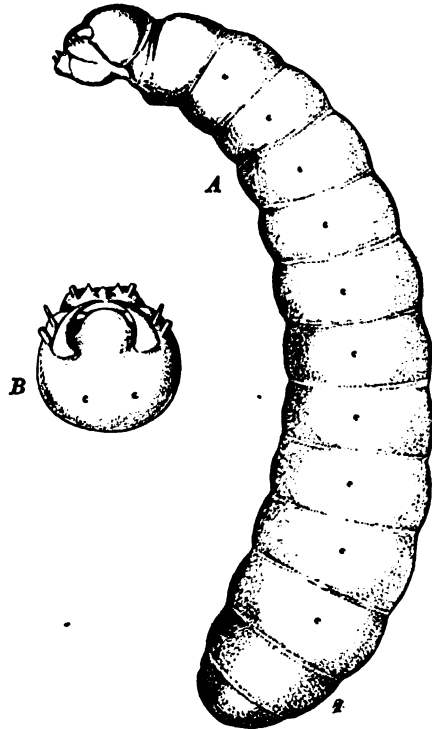


FIG. 3. *A*, nearly adult larva of *Megaponera farctens* Fabr.; *B*, head of same, dorsal view.

of the Ponerinæ are fed with liquid food regurgitated on their mouths by the workers. Miss Fielde thus describes the process in *Aphanogaster* (1901):

The feeding of the larva, which is bent nearly double in the egg, with regurgitated food begins as soon as it straightens itself and protrudes its mouth. When the larvæ begin to appear in the egg-packet, the workers lift the packet and hold it free and still, while one of their number holds a translucent white globule of regurgitated food to the larval mouth projecting from

the surface of the egg-packet. I have repeatedly seen the workers thus feeding the very young larvæ, a single globule of regurgitated food serving for a meal of which four or five larvæ successively partook.

Undoubtedly the majority of Myrmicinæ, Dolichoderinæ and Camponotinæ, the three most highly specialized subfamilies of ants, feed the brood throughout its larval stages with regurgitated liquids. Concerning larval feeding in the Dorylinæ nothing is known.

I come now to a consideration of some of the ant larvæ collected by Mr. Lang in the Belgian Congo. Four of these, all belonging to the subfamily Myrmicinæ, are of unusual interest. One of the species is a new *Pædalagus* which I shall describe elsewhere as *P. termitolestes* sp. nov., the third of the genus to come to light, as only one Indian and one other West African species were previously known. The workers of *termitolestes* are minute brownish yellow ants which live in the masonry of large termite hills and undoubtedly prey on their inhabitants. Their habits therefore resemble those of the well-known thief-ants, *Solenopsis molesta* of North America and *S. fugax* of Europe. The larva (Fig. 5) has a singular shape, being almost spherical, with a short neck, small head and minute, bidenticulate mandibles. The delicate integument is studded with very short, stiff hairs, each of which has two recurved branches. The larvæ, which are held together in compact masses by the interlocking of these hooked hairs, are fed with liquid food by regurgitation as is evident from the contents of their large spherical stomachs and the very feeble development of their mouthparts. Although, like other Myrmicinæ, they do not spin cocoons but form naked pupæ, they nevertheless possess huge salivary glands. Even in the very young larva (Fig. 5A) the salivary receptacle on each side is full of a clear liquid secreted by the large cells of the two branches of the gland. In the nearly full-grown female larva (Fig. 5B) the glands are very voluminous and have their lumen and that of the receptacle full of secretion shown as dark, compact masses in the figure, which was, of course, drawn from a specimen hardened and dehydrated in alcohol. As such an amount of saliva would hardly be necessary for digestive purposes and as it is not used in the form of silk by the full-grown larva, it probably serves as a store of food for the nurses. The *Pædalagus* larvæ, therefore, would

seem to resemble the repletes of honey ants (*Myrmecocystus*, *Leptomyrme*, etc.), except that the food for the workers is metabolized and stored as saliva by the larva, instead of merely being ingurgi-

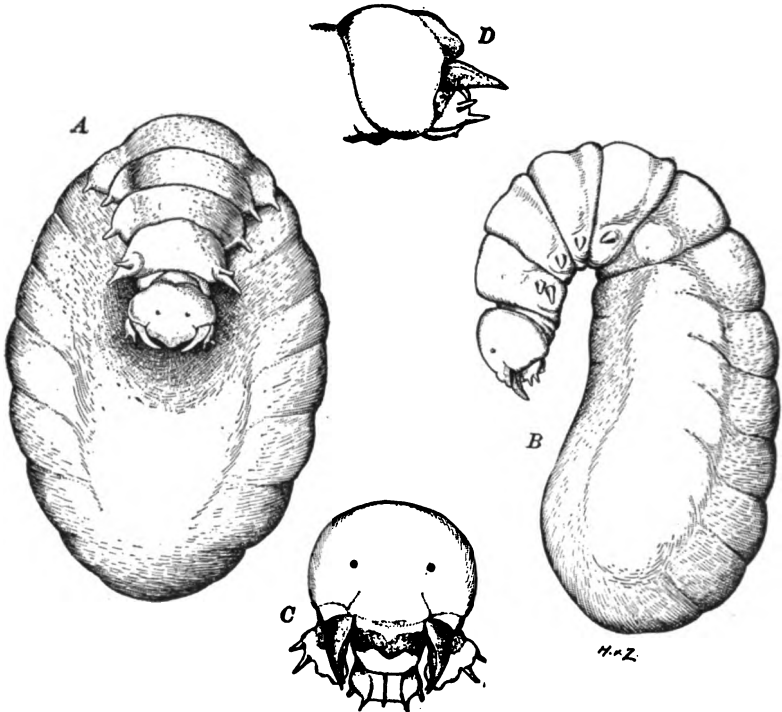


FIG. 4. Adult larva of *Bothroponera sublaevis* Mayr. A, ventral; B, lateral view; C, head, dorsal view; D, head, in profile.

tated and stored in the ingluvies, or crop by a certain number of workers. From the fact that other Myrmicine ants, although they spin no cocoons, often have well-developed salivary glands, we may infer that these organs have much the same function as in *Pædalgus*. To prove this, however, additional observations are necessary, though other reasons for believing it to be the case, will appear in the sequel. In all the larval stages of the Dolichoderinæ and in the immature larvæ of Camponotinæ the salivary glands are probably put to a similar use. In the species of *Æcophylla* and *Polyrhachis* that employ their young larvæ for spinning the silken portions of

the nest inhabited by the whole colony, we must suppose that the spinning habit, which in other Camponotine ants is manifested only at the end of larval life, has become secondarily precocious, but even in such larvæ the saliva in the stages immediately after hatching may, perhaps, still serve as an agreeable draught for the nurses.

The three remaining larvæ which I wish to describe belong to species formerly included in the genus *Sima* but now for taxonomic

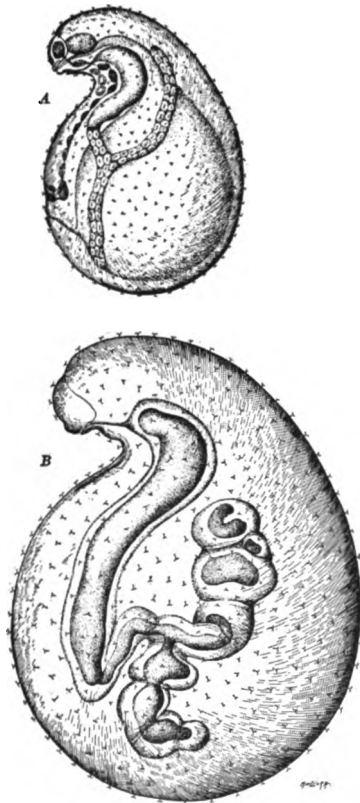


FIG. 5. *A*, very young; *B*, nearly adult larva of *Padalgus termitolestes* sp. nov.; lateral view to show the development of the salivary glands.

reasons referred to *Tetraponera* and *Pachysima*. These ants live in hollow twigs like the species of the closely related neotropical genus *Pseudomyrma*. A large collection of *Tetraponera tessmanni*, made by Mr. Lang, included larvæ and pupæ in all stages of de-

velopment. The adult larva differs little from the youngest and is shown in Fig. 6. It is long, cylindrical and hypocephalic, *i. e.*, with the head on the ventral side instead of being terminal. Unlike the various larvæ described above, it has a pair of swollen appendages, belonging to the prothoracic segment and applied to the sides of the

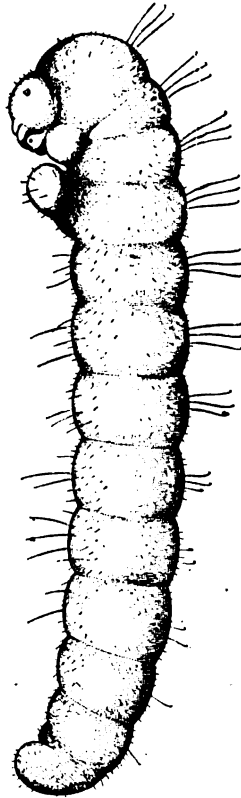


FIG. 6. Adult larva of *Tetraoponera tessmanni* Stitz.

head, and a large protuberance, evidently representing a pair of fused appendages, on the ventral side of the first abdominal segment. The dorsal surface is furnished with long, hook-shaped hairs, by means of which the larva is evidently suspended from the walls of the nest in the same manner as some of our American ant larvæ (*Pheidole*, *Leptothorax*, etc.) which have similar dorsal hairs.

Other larvæ of *Tetraponera* (*natalensis*, *allaborans*, etc.) are not unlike those of *T. tessmanni*.

The meaning of the thoracic and abdominal appendages becomes clear when we examine the larvæ of *Pachysima æthiops* and *latifrons*. Four distinct stages, probably separated by moults, or ecdyses, may be recognized in *æthiops*. The first stage larva, just after hatching, is represented in Fig. 7 as it appears in ventral and

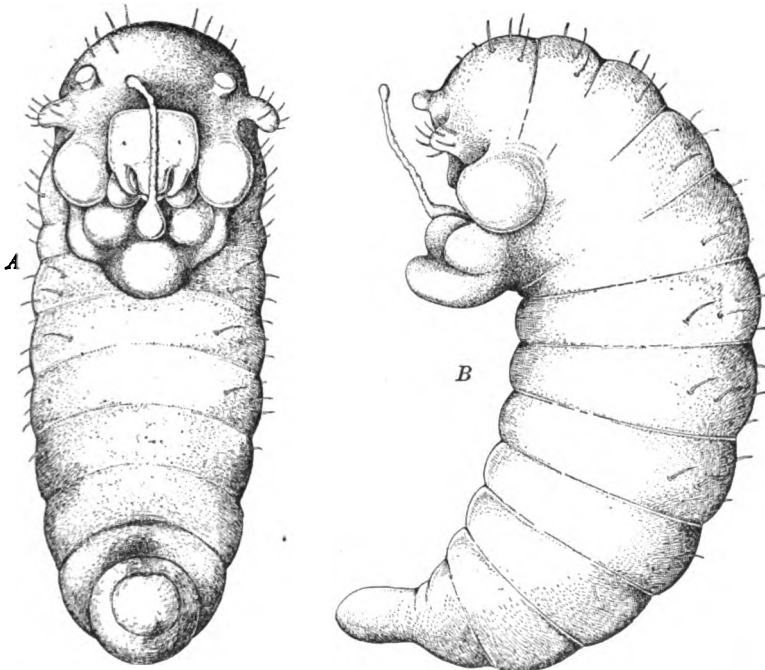


FIG. 7. First larva stage ("trophidium") of *Pachysima æthiops* F. Smith. A, ventral; B, lateral view.

lateral view. The body is curved, convex dorsally and concave ventrally, and terminates behind in a cylindrical projection, with the anus shifted to the ventral surface near its base. The creature is strongly hypocephalic like the larval *Tetraponera* and *Pseudoponera*. The head is surrounded by a cluster of prominent, tubercle-like appendages. On the prothorax, which is large and forms a great hood over the head, there are three pairs of these appendages, an anterior truncate pair, a median pointed pair and a large posterior pair,

swollen and rounded and embracing the sides of the head. These evidently correspond to the single prothoracic pair of the *Tetraponera tessmanni* larva. The mesothoracic segment has a pair of smaller appendages nearer the mid-ventral line. Between them arises a very peculiar organ with a swollen, pear-shaped base prolonged into a slender, apparently erectile, tentacle-like process which extends up in front of the head and terminates in a small ampulla. The first abdominal segment bears a pair of large swollen appendages lying at the base of the mesothoracic pair and united with a large and very prominent mid-ventral tubercle. This tubercle and its lateral appendages are represented in the *T. tessmanni* larva but the others, with the exception of the third prothoracic pair, are absent. Sections and stained, cleared preparations of the whole larva show that the various tubercles contain portions of the fatbody, at least in the bases of their cavities, and next to the hypodermis a dense, granular substance, evidently a coagulated liquid produced by the underlying adipocytes, or trophocytes. The same liquid also fills the unpaired tentacle, except its pear-shaped base, which contains fat cells. Around the bases of the tubercles are muscles so arranged that their contraction must increase the pressure on the fat and granular liquid and in all probability cause the latter to exude through the hypodermis and delicate chitinous cuticle onto the surface. The whole arrangement of the tubercles, in fact, constitutes a system of exudate organs, or exudatoria, as I shall call them, adapted to secrete substances that can be licked up by the ants when they are feeding and caring for the larvæ. In this stage the mandibles are small, soft, blunt and unchitinized so that the larva must be fed with regurgitated liquid food. The labium has a peculiar pair of fleshy appendages, shown just beneath the mandibles in 7A. The body is naked, except for a few sparse, pointed bristles on the dorsal surface and the median pair of prothoracic appendages. As nothing like this larval stage is known among ants or indeed among the Hymenoptera, I propose to call it the "trophidium."

The second stage larva is shown in Fig. 8A. The various exudatoria are smaller in proportion to the remainder of the body but are still much like those of the trophidium. The body is more elliptical, the mandibles are more pointed and distinctly falcate, but even in

this stage they are unchitinized and therefore nonfunctional. The coarse hairs are visible on the dorsal surface but a more uniform investment of small hairs has made its appearance. They are blunt or even clavate, especially on the prothoracic segment. In this and the trophidium stage I am unable to find any salivary glands in cleared preparations though rudiments may, perhaps, be present.

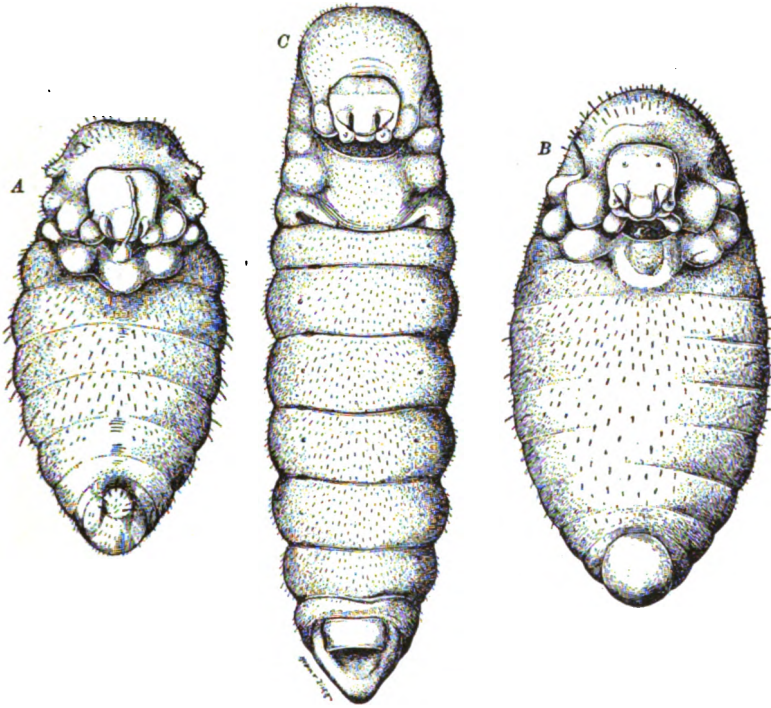


FIG. 8. *A*, second, *B*, third and *C*, fourth (adult) larval stages of *Pachysima æthiops* F. Smith.

The third stage larva (Fig. 8*B*) is larger and very regularly elliptical. The exudatoria can all be recognized, except the unpaired tentacle. It is, however, present in some of the younger individuals but in a greatly reduced and vestigial condition and at the bottom of the deep depression which now appears as a definite pocket just back of the mouth and under the midventral swelling of the first abdominal segment. In many larvæ I found in this pocket a small,

rounded, dark-colored pellet, which puzzled me at first. In sections, however, it was at once seen to consist of the triturated and compacted bodies and parts of small insects. It is, in fact, a food-pellet placed by the worker ants in the pocket just behind the larva's mouth. In this stage, therefore, the larva is fed on solid food and the strongly chitinized, acute and bidentate mandibles corroborate this statement. Slender salivary glands may also be detected, indicating that the substance of the food-pellet is subjected to extraintestinal digestion. The longer hairs on the dorsal integument have almost completely disappeared. The first pair of appendages on the prothorax has disappeared and the second pair is obsolescent.

In the fourth, or adult stage (Fig. 8C) the larva is more elongate and cylindrical and much more hypocephalic, the prothorax forming a great protuberance in front of the head. The exudatoria are still recognizable, with the exception of the first and second prothoracic pairs, which have disappeared entirely. The labial appendages are reduced. A food pellet was found in the postcephalic pocket in several of the larvæ of this stage but is not represented in the figure. The coarse hairs have disappeared from the integument, which is now uniformly covered with very short, delicate hairs, and the structure of the posterior end of the body is very different from that of the preceding stages.

We owe the only account of the *athiops* larva in the literature to Emery (1912). He describes what corresponds to my fourth stage larva very briefly and figures its anterior end with some of the exudatoria, but erroneously interprets the large prothoracic pair as "ébauches de pattes," or rudiments of the anterior pair of imaginal legs.⁴

The larvæ of *Pachysima latifrons* are quite as extraordinary as those of *athiops* and also pass through four stages. The trophidium, or first stage, shown in Fig. 9, is very hypocephalic, the pro-

⁴ In the same paper Emery created the subgenus *Pachysima* for the accommodation of what was formerly called *Sima athiops* and for a new species described as *latifrons*, because they have the frontal carinæ of the worker and female much more widely separated than in the numerous species of *Tetraponera* (*Sima auctorum*). I have raised *Pachysima* to generic rank, because the larvæ of the two species are so very different from those of *Tetraponera*.

thoracic segment being greatly enlarged and projecting anteriorly. Both preparations stained *in toto* and sections show that the portion of the fat-body in this segment is sometimes heavily charged with urate crystals, so that it undoubtedly functions as a storage kidney till the Malpighian vessels are sufficiently developed to excrete. The first and second pairs of prothoracic appendages of the *æthiops* larva are absent, but the third pair is very large and embraces the sides of the head. The meso- and metathoracic segments each bear a pair of slender pointed appendages, the first abdominal segment a

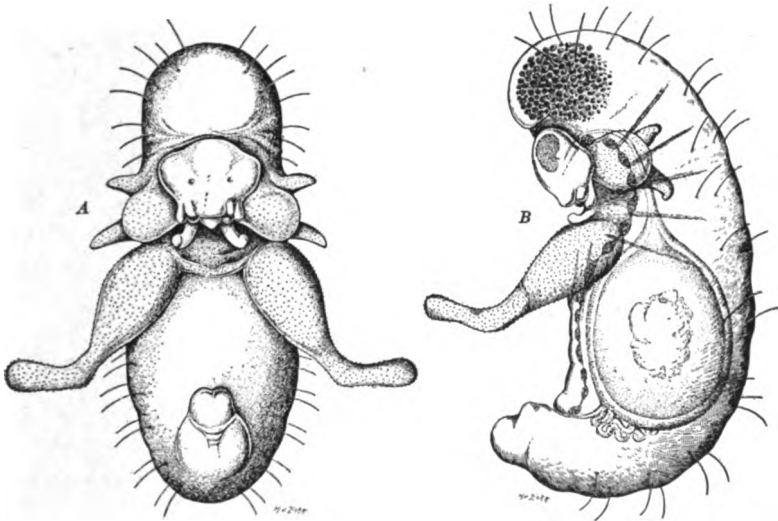


FIG. 9. First larval stage ("trophidium") of *Pachysima latifrons* Emery. A, ventral; B, lateral view.

huge leg-like pair, which are swollen and fusiform at the base and run out into a long slender process which forms an obtuse angle with the basal portion. The sternal region between these appendages is protuberant and its cuticular covering, like that of the four pairs of appendages is minutely prickly, unlike the smooth cuticle of the remainder of the body. Sections show that both the appendages and the sternal swelling are exudate organs, though the prothoracic and abdominal pairs are much more important than the others. The prothoracic appendages are filled with blood and very

little fat tissue, but their hypodermis is much thickened and consists of crowded cells arranged in peculiar clusters. In section the abdominal appendages appear as in Fig. 10. The fusiform base is filled with large, clear trophocytes, or fat-cells, some of which in the middle of the swelling may contain urate crystals, like those in the prothoracic storage kidney, but the slender, tubular distal portion contains a granular liquid, which can only be regarded as an exudate

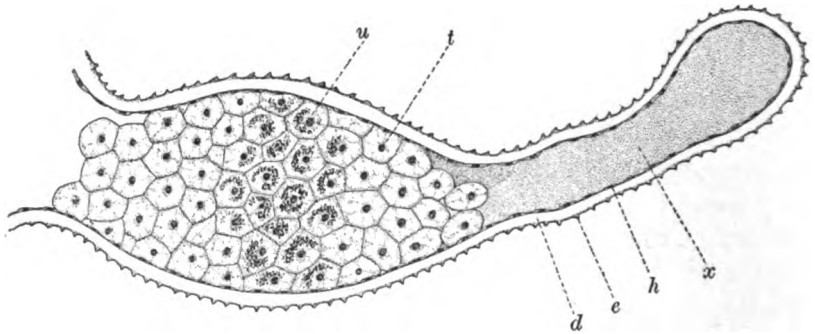


FIG. 10. Longitudinal section through exudatorium of first abdominal segment of trophidium of *Pachysima latifrons* Emery.

derived from the trophocytes in the basal enlargement. This exudate is evidently filtered through the thin cuticula covering the appendage by pressure, for there is a rather elaborate system of muscles, as in the *athiops* larva, surrounding the bases of the appendages and capable of subjecting their contents to pressure. The head is small and has soft, blunt, rudimentary and unchitinized mandibles, and the labium bears a pair of long, palp-like appendages, which project forward in the deep depression between the head and the swollen sternal portion of the first abdominal segment. These are probably also exudatoria and seem roughly to correspond to the unpaired tentacle of the *athiops* larva. The structure of the mouth-parts shows that the larva in this stage is fed with liquid food regurgitated by the workers. The convex dorsal surface is beset with sparse, curved bristles of uniform thickness, with blunt tips. The segmentation of the body is indistinct and its posterior end curves forward and terminates in a large tubercle with the anal orifice just anterior to its base. Fig. 9B, drawn from a stained and cleared

preparation, shows the nervous system and alimentary canal. The Malphigian vessels have only just begun to develop at the blind end of the proctenteron where it abuts on the posterior end of the large, elliptical mesenteron, or stomach, but no salivary glands can be detected.

In the second stage larva (Fig. 11*A*) the body is more elongate and cylindrical and the four pairs of appendages can still be recog-

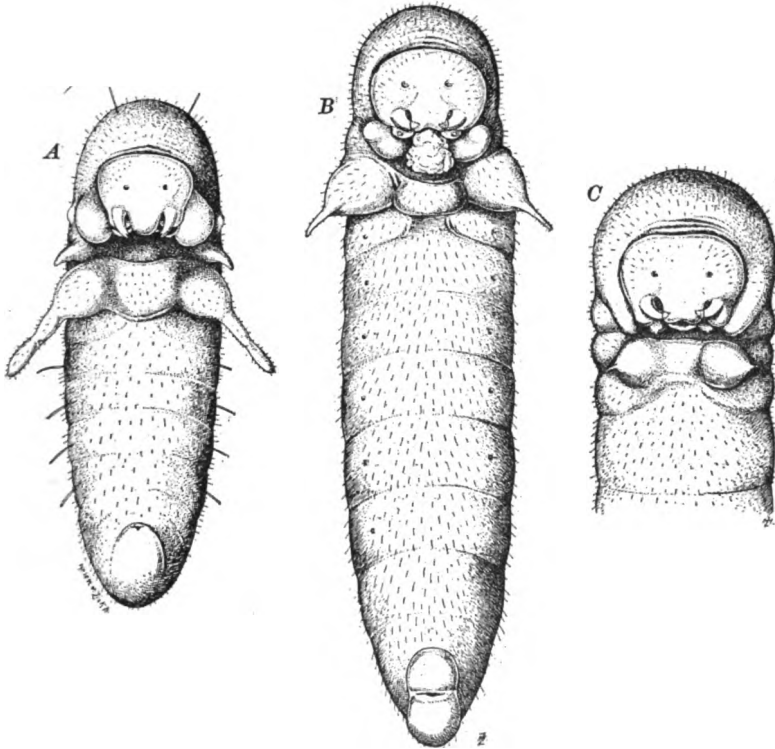


FIG. 11. *A*, second, *B*, third and *C*, fourth (adult) larval stages of *Pachysima latifrons* Emery.

nized though considerably smaller in proportion to the remainder of the body. The mandibles are becoming chitinized. Many of the long hairs on the dorsal surface are still present but a general covering of short, sparse hairs has made its appearance.

The third stage larva (Fig. 11*B*) is larger and still more elongate

and cylindrical and shows a further regressive development of the exudatoria. Those on the meso- and metathoracic segments have disappeared and the abdominal pair has short broad bases with the distal portions attenuated to slender points. The labial appendages have also disappeared. The mandibles are well chitinized and the larva is now fed with pellets of crushed insects, like the *æthiops* larva in the corresponding stage. These pellets were found *in situ* in several of the alcoholic specimens as represented in Fig. 11B. The pellet lies in the deep pocket between the head and the sternal protuberance of the first abdominal segment and is therefore within easy reach of the mandibles and labium of the larva. Cleared preparations show that the salivary glands have made their appearance, though they are small and slender.

The anterior end of the fourth stage, or adult larva is shown in Fig. 11C. The exudatoria of the prothoracic segment now appear merely as a pair of welts or folds embracing the sides of the head and continuous with the more dorsal portions of their segment, which is relatively smaller and less projecting than in the preceding stages. The exudatoria of the first abdominal segment are still distinct but their distal portions are reduced to mere points, sometimes absent in larvæ just before pupation, and the sternal swelling is much less prominent. In this stage the larva resembles that of *Tetraponera* throughout its various stages. In the third and fourth stages of the *latifrons* larva, as in the corresponding stages of *æthiops*, the salivary glands probably furnish secretions which are useful both in the extraintestinal digestion of the food pellet and as substances that can be imbibed by the workers. The fact that in the two species of *Pachysima* the exudatoria decline *pari passu* with the development of the salivary glands certainly suggests that both sets of organs have to some extent a common function. In forms like *Pædalagus* and probably many other Myrmicinae, in which the development of the salivary glands is more precocious, the exudatoria are not developed.

I believe, therefore, that we must interpret the exudatoria as very primitive glands, but they differ so much from the ordinary hypodermal glands of insects that it will be necessary to consider them more closely before proceeding further. They are, as we have seen, small

diverticula like the embryonic legs, consisting of hypodermis and its overlying cuticula and containing a portion of the fat-body separated from the hypodermis by a granular liquid.⁵ Now the fat-body of insects may be regarded as a diffuse ductless gland, the cells (trophocytes) of which take certain substances from the blood in which they lie, store them in the cytoplasm as fat-globules or proteid granules and later return them to the blood in a more finely divided, if not chemically modified form. The exudate which accumulates in the distal ends of the exudatoria is therefore merely blood charged with nutrient substances from the fat-cells, and either filters gradually through the hypodermis and overlying cuticle or is forced through them by muscular pressure. At first sight it would seem that the cuticle must be impervious to such a liquid, but a consideration of the more recent work on the minute structure of chitin by Holmgren (1901, 1902), Biedermann (1902, 1903), Kapzov (1911), Casper (1913) and others shows that there is nothing to prevent the passage of a thin fatty liquid, even if it were not under pressure and even if the cuticle were much thicker than it is in the ant larva. The cuticle is a colloid, either of a reticular structure, as Kapzov believes, or formed of horizontal layers of very fine fibrillæ crossing one another at an angle of 60° as most investigators, including Biedermann and Casper, maintain. Between the fibrillæ are regularly distributed and extremely fine openings or "pore canals," through which a liquid might readily pass as if the cuticle were a

⁵ The question arises as to whether the larval exudatoria of *Pachysima* are the homologues of the true appendages on the thoracic and first abdominal segments of embryo insects. In other words, do the exudatoria represent true legs or are they new formations? The trophidium of *P. latifrons* seems to point to the former alternative. The large leg-like exudatoria on the first abdominal segment are certainly very suggestive of the embryonic "pleuropodia" to which I devoted a paper many years ago (1890). On the other hand, the four pairs of trophidium appendages in *latifrons* seem to be homologous with the four pairs of papillæ in the larva of *Bothroponeura* (Fig. 4), and the latter are almost certainly merely remnants of a considerable number of similar papillæ which are scattered over the whole surface of the larval *Pachycondyla*, *Diacamma* and *Ponera*. Furthermore, two of the pairs of exudatoria on the prothorax of the *Pachysima athiops* trophidium and the unpaired tentacle-like exudatorium just behind the head cannot be brought into the homology. It would seem, therefore, that the exudatoria must be regarded as cœnogenetic, or new formations peculiar to the young larvæ of certain Old World genera of Pseudomyrmini.

filter. Even in the case of the hypodermal glands fatty liquids are known to pass through the thin chitinous cuticle with which the secreting surface of the cytoplasm is always covered, even where the ends of the ducts are intracellular.

In this connection attention may be called to a very similar exudation of blood plasma charged with certain substances (*e. g.*, cantharidin) through the hypodermis and cuticle in many Meloid, Cantharid, Lampyrid, Coccinellid and Chrysomelid beetles. It has long been known that when these insects are roughly handled they discharge from the articulations of their legs a white, yellow or greenish, bad-smelling liquid, which Magretti (1881, 1882), Lutz (1895), De Bono (1889) and Berlese (1909) have shown to be blood plasma. It accumulates in pockets at the articulations after passing through the integument and leaving the blood cells (amœbocytes) behind, and is clearly an exudate though it is repugnatorial instead of having an alluring or nutrient function like the blood plasma of *Pachysima*.

It is unnecessary, however, to seek confirmation of my interpretation of the circumoral appendages of the *Pachysima* larva by merely pointing to the conditions in the Meloids, Coccinellids, etc. Wasmann, Holmgren and Trägårdh have published valuable studies of exudate organs much more like those of the ant larvæ. To Wasmann (1903) belongs the credit of having first made an extensive investigation of the trichome glands and exudatoria of numerous myrmecophiles and termitophiles. Many of these structures are more or less modified hypodermal glands with tenuous ducts opening at the base of hairs (trichomes) which either diffuse the secretion so that it can evaporate quickly or spread it out so that it can be readily licked up by the ants, but in such termitophiles as the Staphylinid beetle *Xenogaster inflata*, the fat-body in certain parts of the abdomen forms "blood tissue," which becomes the "exudate" by passing through a layer of hypodermis at the base of papillæ ("exudate buds").⁶ The latter seem to consist of cuticular substance perforated by delicate canals that conduct the exudate to the surface. Wasman says:

The exudate of these buds seems therefore to be a component of the blood fluid, which is as it were filtered through the hypodermal layer.

⁶ The trichome glands may be compared with similar structures in other

Some of the details in his account and figures are far from clear, but there can be no doubt about his meaning. Equally interesting is his description of the larvæ of certain symphilic myrmecophiles (*Lomechusa*, *Atemeles* and *Xenodusa*) concerning which he writes:

The cuticula of the whole body, excepting the head, is membranous and whitish. Outer exudate organs (*i. e.*, trichomes) are lacking. The exudate tissue is exclusively the fat-body.

He believes, in other words, that in these larvæ the voluminous fat-body functions as a huge exudatorium which pours a fatty exudate onto the surface of the body. This at once suggests that in many ant larvæ the general fat-body may have the same function, so that there would be in these insects three possible sources of liquid substances agreeable to the worker ants. the salivary glands, the exudatoria *sensu stricto* and the fat-body. They would not all be equally developed in any given species, but at any rate there is just as much reason for supposing that the general fat-body may function as an exudate organ in the ant-larva as in the larvæ of the *Lomechusine* myrmecophiles. Krüger (1910) and Jordan (1913) have cleared up some of the obscurities in Wasmann's paper, especially in regard to the trichome glands of hypodermal origin, but in my opinion have not invalidated his general conclusions in regard to the role of the fat-body and blood in exudation.⁷

animals. Many nonmyrmecophilous insects have similar glands that serve to diffuse sexually attractive secretions. The question arises as to whether many of the hair-tufts in mammals may not have an analogous function. Anthropologists seem not to have explained the retention of hairs in the axillary and pubic regions of man. It is evident that the hairs in the arm-pits serve rapidly to diffuse and evaporate the secretions of the sudorific glands. The pits full of trichomes on the thorax of many symphilic Paussid beetles are strangely suggestive in this connection. The function of the public hairs is not so clear, but perhaps certain bats which have peculiar tufts about the genitalia (see, *e. g.*, the figures of the Congolese *Hipposideros langi* Allen in *Bull. Amer. Mus. Nat. Hist.*, 37, 1917, pp. 436, 437) may indicate that in the remote past the pubic hairs had a sexual function in the ancestors of man.

⁷ For a critique of Jordan's work and for further discussion of the structure and development of *Lomechusa* and *Atemeles* the reader is referred to Wasmann's recent monograph: "Neue Beiträge zur Biologie von *Lomechusa* und *Atemeles*" (1915).

Wasmann has shown in a number of papers that the true guests of termites, the symphiles, are physogastric, *i. e.*, have the abdomen enormously distended with fatty tissue. This condition is very striking in certain Staphylinids (*Xenogaster*, *Corotoca*, *Spirachtha*, *Termitomimus*, etc.) and Diptera (*Timeparthenus*, *Termitomyia*, *Termitoxenia*, *Thaumatoxena*, etc.). Trägårdh (1907) has studied sections of the beetle *Termitomimus*, which lives in considerable numbers in the *Eutermes* colonies of Zululand. His description of the exudate organs is so much clearer than Wasmann's and so significant in connection with my account of the *Pachysima* larvæ, that I quote the greater part of it:

The relation of the fat-body to the hypodermis and the cuticle is different in different parts of the body.

1. The hypodermis is exceedingly thin, sometimes scarcely discernible and pressed close to the cuticle by the underlying fat-body. The cuticle has no distinct endostracum and is penetrated by an immense number of extremely fine pores, arranged in transverse rows. This is the case with the ventral, lateral and posterior part of the pseudoabdomen, *i. e.*, *exactly where the cuticle is of a bright reddish-yellow color* ("symphilous color" Wasmann) *and where the termites may most easily get access to it.*

2. The hypodermis is thick and withdrawn from the cuticle which is thicker, with well-developed epiostracum and endostracum, leaving a rather wide space, which is filled with liquid. . . . The fat-body is contiguous to the hypodermis. The space between the cuticle and the hypodermis is more or less filled with a cyanophilous tissue of a spongy appearance which sometimes exhibits a very distinct radial structure, sometimes is concentrically stratified and contains numerous granules which are also to be found in the trichogenic cells. This is evidently a fluid, which has either passed through the hypodermis and is a derivative from the fat-body or it is a secretion produced by the hypodermis and is coagulated by the method of fixation. . . .

The above stated facts concerning the relation of the fat-body to the hypodermis and the cuticle differ in some essential respects from what Wasmann has found in the termitophilous physogastrous insects studied by him. In *Spirachtha*, *Termitoxenia*, the larvæ of *Orthogonius* and *Glyptus*, in *Xenogaster* and other Aleocharini the hypertrophied fat-body is always surrounded by large tracts of blood-tissue, consequently the exudation is derived directly from the blood-tissue and only indirectly from the fat-body. The exudation is no fluid but evaporates through the membranous cuticle, which has no pores.

To support the theory of the exudation being only an attractive odor and not offering the termites any source of subsistence Wasmann points out the fact that the symphiles as a rule only occur in small numbers in the nests.

These statements, however true they may be with regard to the above mentioned genera, do not apply at all to *Termitomimus*. In this genus on the

contrary, in the part of the abdomen which is easiest accessible to the termites, viz., the ventral, lateral and posterior side of the pseudoabdomen,

1. The fat-body is not surrounded by the blood-tissue but contiguous with the extremely thin hypodermis and

2. The cuticle is penetrated by an immense number of pores (and the endostracum is not distinctly discernible).

3. Furthermore *Termitomimus* does occur in great numbers in the nests of the termites.

These facts seem to me to suggest that in *Termitomimus* the fat itself or a derivate of the fat-body may possibly be secreted as a fluid through the numerous pores of the cuticle and not merely evaporate and that *Termitomimus* thus offers to the termites a source of subsistence. The comparatively very large extension of the area of the cuticle which exhibits this structure also argues in favor of this theory.

In another paper (1907a) Trägårdh describes a peculiar Tineid caterpillar with exudatoria even more like those of the *Pachysima* larva. He found it in the tree nests of *Rhinotermes* in Zululand. The relations between the caterpillar, which feeds on the woody substance of the nest, and the termites are evidently friendly.

When disturbed, the larvæ were seen to make their way to other parts of the nest, coming along one after the other, with regular intervals, like in a procession, each larva being escorted by a few soldiers and workers.

Each of the seven anterior abdominal segments of the caterpillar bears on its sides a pair of long, tapering appendages, which Trägårdh regards as exudatoria and each appendage contains a lobe of the fat-body, surrounded by blood. The imperforate hypodermis is separated from the thin cuticle, the space between being filled with exudate. In this case he believes that the exudate must evaporate on the surface of the body, since he says:

As the larva emits a strong odor, and the termites were scarcely seen touching the appendages, the exudation is very likely an alluring odor.

He compares the organs with the various osmateria described by Packard in the caterpillars of *Megalopyge* and *Hemileucidæ*.

Certain organs in the larvæ of two groups of Hymenoptera may also be interpreted as exudatoria. In 1907 I called attention to peculiar blister-like organs on the sides of pseudonymphs of certain Eucharine parasites of ants, notably in *Orasema*. These structures are shown in Figs. 19 and 21, Pl. 2 of the paper referred to and in Fig. 251 F, G, p. 415 of my ant book (1910). In the pupa of the

same insect the abdomen has similar organs in the form of transverse welts. Reichensperger (1913, Pl. 6, Fig. 12) describes and figures the very same organs in an Abyssinian Eucharine, *Psilogaster fraudulenta*, which lives with *Pheidole megacephala*, and suggests that they may be exudate organs. Forel (1890) had previously mentioned similar structures ("asperités et boussoufflures") on the pupa of the large *Eucharis myrmeciae* taken from the cocoon of an Australian bulldog ant, *Myrmecia forficata*. On recently reexamining my preparations I find that the organs of *Orasema viridis* may be interpreted as exudatoria. They are knob-shaped, with very thin hypodermis and cuticle and are filled with blood but contain no fat-tissue, although the fat-body in the abdomen and thorax is very voluminous. In life the knobs are colorless and glistening. Both the pseudonymphs and pupæ are assiduously licked by their host, *Pheidole instabilis*, so that the knobs of the former and the welts of the latter probably produce substances agreeable to the ants.⁸

The other group of Hymenoptera comprises the singular South African bees of the genus *Allodape*. In 1902 Brauns showed that they make very primitive nests, consisting of a single cavity, often 12 cm. long, in the stems of various Liliaceous plants, but unlike all other solitary bees, feed their larvæ from day to day with "Futterbrei" (honey-soaked pollen?). In the warmer portions of Cape Colony and German Southwest Africa *Allodape* breeds throughout the year. The single cavity of the nest contains eggs, larvæ in all stages, pupæ and freshly emerged bees intermingled. The larvæ are unique among bees in possessing peculiar tubercles on the sides of the fifth to tenth segments. Friese (1914) publishes photographs of some rather shrivelled half-grown larvæ and describes the tubercles as "bladderlike evaginations of the outer skin." Brauns seems to regard them as legs (pseudopods) and says that they are used to hold the food, but it seems probable that they are really

⁸ While this paper was in the hands of the printer Dr. R. J. Tillyard of New South Wales sent me the larvæ, pupæ and an adult male of a huge undescribed Eucharine, which he found attacking the brood of the red bulldog ant (*Myrmecia gulosa*). Prof. C. T. Brues believes that the parasite may belong to the genus *Psilogaster* and will describe it in the near future. The larvæ and pupæ are covered with exudatoria like those of *Orasema* but more prominently developed.

exudate organs. If this proves to be true, the resemblance of *Allodape* to *Pachysima*, which also rears its brood in all stages in hollow stems and feeds the older larvæ with food-pellets, would be very striking. *Allodape* is also of considerable interest in connection with Roubaud's observations on the wasp *Synagris* which will be considered in the sequel.

More important in their bearing on the exudate organs of *Pachysima* are Holmgren's observations on the termites. He devotes the twelfth chapter of his volume (1909) on the anatomy of these insects to the exudate tissue. Termites are really themselves physogastric like their guests, and Holmgren shows that all the castes, but especially the queens, have extensive exudate tissues, consisting of the peripheral layers of the abdominal fat-body. In these layers the trophocytes do not contain fat-globules but numerous minute granules which are discharged into the blood and thus convert it into the exudate that passes through numerous pores or lacunæ in the chitinous cuticle to the surface. There it is licked up by other members of the colony. He finds that the development of the exudate tissue differs considerably not only in the different castes but also in their various developmental stages and

that the intensity of the licking and feeding of the individuals of a termite colony is directly proportional to the amount of their exudate tissue. Those with the largest mass of exudate tissue are the best fed and the most licked. In other words, the care bestowed by the workers on the various members of the colony is not an immediate expression of an altruistic philoprogenitive instinct (Brutpflegeinstinct), but depends essentially on egoistic motives, *i. e.*, exudate hunger.

To this point I willingly follow Holmgren, but both he and Wassmann have used their respective observations as a basis for what seem to me to be rather dubious speculations, a consideration of which will have to be deferred till the more general part of my discussion is reached.

Escherich (1911) gives a more vivid, not to say more spectacular account of the exudate hunger of termites. So eager are the workers of the Ceylonese *Termes redemanni* for the exudate of their huge physogastric queen that they actually tear little strips out of her cuticle in order to get at the liquid more readily! Escherich found that old queens sometimes have their white ab-

domens dotted with the small brown scars of the wounds thus inflicted by their progeny. Here the feeding behavior of the mother and offspring is the reverse of that in incipient ant colonies, since the queens are fed with regurgitated food by the workers and feed the latter with exudates, but this is, in all probability, also the case in established ant colonies when the workers have matured and the queen no longer feeds the brood.

The facts collated in the foregoing paragraphs relate to the exudate organs, but we had previously seen that the salivary glands of larval ants probably subserve a similar function in the life of the colony in addition to digesting proteid foods extraintestinally and producing silk at the time of pupation. The question arises as to whether there is any evidence that in other groups of social insects the salivary glands of the larva produce substances which are consumed by the worker nurses. Fortunately there are some very pertinent observations at hand in the French literature which is so rich in splendidly original works on the habits and taxonomy of insects. The observations to which I refer relate to the social wasps. Du Buysson (1903) observed that the larvæ of *Vespa* "secrete from the mouth an abundant liquid. When they are touched the liquid is seen to trickle out. The queen, the workers and the males are very eager for this secretion. They know how to excite the offspring in such a way as to make them furnish the beverage." And Janet (1903) was able to prove that the secretion is a product of the salivary, or spinning glands and that it flows from an opening at the base of the labium. "This product," he says, "is often imbibed by the imagines, especially by the just emerged workers and by the males, which in order to obtain it, gently bite the head of the larva."

The most illuminating study of this matter, however, is found in a fine paper by Roubaud on the wasps of Africa (1916). His account of the primitive wasps of the genus *Belonogaster* presents a striking picture of one of the earliest stages in the social life of wasps, as will be seen from the following quotation:

In the species of *Belonogaster* as well as in those of the genera *Icaria* and *Polistes* we have been able to observe this proceeding in detail. All the larvæ, from birth, secrete from a projection of the hypopharynx, on the inferior surface of the buccal funnel, an abundant salivary liquid, which at the slightest touch spreads over the mouth in a drop. All the adult wasps,

males as well as females, are extremely eager for this salivary secretion, the taste of which is slightly sugary. It is easy to observe, especially in *Belonogaster*, the insistent demand for this larval product and the tactics employed to provoke its secretion.

As soon as a nurse wasp has distributed her food pellet among the various larvæ, she advances with rapidly vibrating wings to the opening of each cell containing a larva in order to imbibe the salivary drop that flows abundantly from its mouth. The method employed to elicit the secretion is very easily observed. The wing vibrations of the nurse serve as a signal to the larva, which, in order to receive the food, protrudes its head from the orifice of the cell. This simple movement is often accompanied by an immediate flow of saliva. But if the secretion does not appear the wasp seizes the larva's head in her mandibles, draws it towards her and then suddenly jams it back into the cell, into which she then thrusts her head. These movements, involving as they do a stimulation of the borders of the mouth of the larva, compel it to secrete its salivary liquid.

One may see the females pass back and forth three or four times in front of a lot of larvæ to which they have given nutriment, in order to imbibe the secretion. The insistence with which they perform this operation is such that there is a flagrant disproportion between the quantity of nourishment distributed among the larvæ by the females and that of the salivary liquid which they receive in return. There is therefore a real exploitation of the larvæ by the nurses.

The salivary secretion may even be demanded from the larva without a compensatory gift of nourishment, both by the females that have just hatched and by the males during their sojourn in the nest. The latter employ the same tactics as the females in compelling the larvæ to yield their secretion. They demand it especially after they have malaxated an alimentary pellet for themselves, so that there is then no reciprocal exchange of nutritive material.

It is easy to provoke the buccal secretion of the larvæ artificially. Merely touching the borders of the mouth will bring it about. The forward movement of the larvæ at the cell entrance, causing them to protrude their mouths to receive the food pellet, is also easily induced by vibrations of the air in the neighborhood of the nest. It is only necessary to whistle loudly or emit shrill sounds near a nest of *Belonogaster* to see all the larvæ protrude their heads to the orifice of the cells. Now it is precisely the vibrations of the air created by the rapid agitation of the bodies of the wasps and repeated beating of their wings that call forth these movements, either at the moment when food is brought or for the purpose of obtaining the buccal secretion which is so eagerly solicited.

Roubaud summarizes the general bearing of his observations in the following paragraph:

The reciprocal exchange of nutriment between the adult females and the larvæ, the direct exploitation of the larval secretion without alimentary compensation by the males and just emerged females are trophobiotic phenomena the elucidation of which is of great importance to an understanding of the

origin of the social tendencies in the Vespidae, as we shall show in the sequel. The retention of the young females in the nest, the associations between isolated females, and the coöperative rearing of a great number of larvæ are all rationally explained, in our opinion, by the attachment of the wasps to the larval secretion. The name *æcotrophobiosis* (from *olkos*, family) may be given to this peculiar family symbiosis which is characterized by reciprocal exchanges of nutriment between larvæ and parents, and is the *raison d'être* of the colonies of the social wasps. The associations of the higher Vespids has, in our opinion, as its first cause the trophic exploitation of the larvæ by the adults. This is, however, merely a particular case of the *trophobiosis* of which the social insects, particularly the ants that cultivate aphids and coccids, furnish so many examples.

It does not seem to me that the term "*æcotrophobiosis*" is aptly chosen. Apart from its length, it implies, as Roubaud states, a relationship between adult and larval members of the same colony or family, comparable with that existing between ants on the one hand and Aphids, Coccids, Membracids and Lycænid larvæ on the other. This relationship, however, is, so far as nutrition is concerned, one-sided since the ants exploit the aphids, etc., and may defend or even transport them, but do not feed them. Moreover, even in *Belonogaster* the feeding of adults and larvæ is reciprocal, and the latter could not be reared if they were actually exploited to such an extent as to interfere with their growth. As the relationship is clearly coöperative or mutualistic, I suggest the term *trophallaxis* (from *τροφή*, nourishment and *ἀλλάττειν*, to exchange) as less awkward and more appropriate than "*æcotrophobiosis*."

That the feeding of the young by the mother wasp without compensation is more primitive than the condition in *Belonogaster* is shown by Roubaud's beautiful observations (1908, 1910, and 1916) on three species of *Synagris* in the Belgian Congo (*callida*, *sicheliana* and *cornuta*). These wasps represent important stages in the transition from the solitary to the social forms, since they make earthen cells like other Eumenids, lay eggs in them and provide the young with paralyzed caterpillars of Hesperid butterflies. In favorable seasons, when caterpillars are bundant, the behavior is like that of our northern Eumenid and Odynerid wasps, numerous small or single large caterpillars being placed with the egg in the cell and the latter sealed up ("approvisionnement massif accéléré"), but when the season is less unfavorable and food scarcer, the wasp's ac-

tivities slow down so that the larva may hatch before all the prey is brought in ("approvisionnement massif ralenti"). This condition leads naturally to a feeding of the larva from day to day with living but paralyzed caterpillars ("éducation surveillée indirecte") and eventually to a stage essentially like that of the social wasps in which the caterpillar is chewed up and placed as a pellet in the mouth of the larva ("éducation surveillée directe"). *Synagris cornuta* has reached this last stage. The mother insect, while malaxating the caterpillar, herself imbibes its juices.

The internal liquids having partly disappeared during this process of malaxation, the prey is no longer, as it was in the beginning, soft and juicy and full of nutriment for the larva. It is possible, in fact, to observe that the caterpillar patée provided by the *Synagris cornuta* is a coarse paste which has partly lost its liquid constituents. There is no exaggeration in stating that such food would induce in larvæ thus nourished an increase of the salivary secretion in order to compensate for the absence of the liquid in the prey and facilitate its digestion.

It is here that the further development to the condition seen in *Belonogaster* and other social wasps sets in. The mother wasp finds the saliva of the larva agreeable and a trophallactic relationship is established. As Roubaud says,

the nursing instinct having evolved in the manner here described in the Eumenids, the wasps acquire contact with the buccal secretion of the larva, become acquainted with it and seek to provoke it. Thence naturally follows a tendency to increase the number of larvæ to be reared simultaneously in order at the same time to satisfy the urgency of oviposition and to profit by the greater abundance of the secretion of the larvæ.

Although considerable evidence thus points to trophallaxis as the source of the social habit in wasps, ants and termites, it must be admitted that the phenomenon has not been observed in the social bees. That the latter may have passed through a phylogenetic stage like that of *Synagris* seems to be indicated by the solitary bees of the genus *Allodape* to which I have already referred (p. 318). Brauns' observations, though meager, show nevertheless that *Allodape* has reached Roubaud's fourth stage, that of direct feeding of the larvæ from day to day, and if I am right in supposing that the peculiar appendages of the larvæ are exudate organs, there would be grounds for assuming that trophallaxis occurs in this case. On

the other hand, it has often been suggested (*e. g.*, by von Buttel-Reepen) that the three social subfamilies, the stingless bees (*Meliponinæ*), bumble-bees (*Bombinæ*) and honey bees (*Apinæ*) have developed from the solitary bees by another and more direct path, for the *Meliponinæ*, though living in populous societies, still bring up their brood in essentially the same way as the solitary bees, *i. e.*, by sealing up the eggs in cells provisioned with honey-soaked pollen. The *Bombinæ*, however, keep opening the cells from time to time and giving the larvæ a little food at a time, and in the honey bee the cells are left open till pupation and the larvæ fed more continuously. Numerous facts indicate that the *Bombinæ* are the most primitive, the *Apinæ* the most specialized of existing social bees, and that the *Meliponinæ*, though closely resembling the solitary bees in the care of the young, are nevertheless in other respects very highly specialized (vestigial sting, elaborate nest architecture, etc.). It is therefore not improbable that these bees, after passing through a stage more like that of the *Bombinæ*, have reverted secondarily to a more ancient method of caring for their brood. At any rate, the *Meliponinæ* have been so little studied, as compared with the *Bombinæ* and *Apinæ*, that they can be left out of the present discussion. Sladen (1912) has given us a good account of the queen bumble bee feeding the larvæ, but he says nothing about the salivary glands of the latter. These are very large, as we know from the work of Bordas (1894), but their development is perhaps fully accounted for by the complete cocoon spun by the mature larva. Even in the honey bee, which has been so thoroughly studied, I find no evidence that the adult workers feed on larval secretions. In both cases, however, it is impossible under natural conditions accurately to observe the behavior of the larva while it is being fed. This might, perhaps, be done if the bees could be induced to rear their young in glass tubes made to resemble the cells.⁹ But even if it should be found, on further investigation, that there is no indication of reciprocal feeding between the larval and adult *Bombinæ* and *Apinæ*, we might still contend that these very highly specialized

⁹ Dr. E. F. Phillips informs me that it would be possible to observe the behavior of honey-bee larvæ and their nurses in cells built against and partly formed by the glass wall of an observation hive.

insects had in their evolution passed far beyond the stages represented by the termites, ants and social wasps. There can, indeed, be little doubt that the bees are descended from wasp-like ancestors and that they must therefore have passed from an animal to a vegetable diet. If the change of diet took place after the social habit had been established, as is possible and as is so clearly shown to be the case in the harvesting and fungus-growing ants, the loss of a resort to the larval secretions by the adult social bees could be readily explained as due to the abandonment of a scarce animal food, procured with considerable difficulty, for nectar and pollen, which are abundant and easily obtained.

Another objection that may be urged against the view that trophallaxis is so fundamental as I contend, is the behavior of the ants towards their inert pupæ, which though transported and defended as assiduously as the larvæ, yield neither liquid exudates nor secretions. This does not seem to me to be a serious objection, because the pupæ evidently have an attractive odor and may therefore be said to produce volatile exudates like certain myrmecophiles. Both the larvæ and pupæ, moreover, evidently represent so much potential or stored nutriment available for the adult ants when the food-supply in the environment of the colony runs very low or ceases entirely. Infanticide and cannibalism then set in with the result that the devouring of the young of all stages may keep the adult personnel of the colony alive till the trophic conditions of the environment improve. Certain predatory tropical species (*Dorylinæ*, *Cerapachyini*) regularly raid the colonies of other ants and carry home and devour their brood. In northern Eurasia and North America *Formica sanguinea* makes similar raids on colonies of *Formica fusca* but permits a certain number of the pupæ to hatch and become "slaves." The latter, however, represent only a small portion of the pupæ secured during the course of the summer. Wasmann believes that the *fusca* pupæ are plundered for the sake of being reared. This I doubt, but if true, we should have to account for it by supposing that to the *sanguinea* workers the odor of the *fusca* pupæ is, if anything, even more attractive than that of their own.

If we confine our attention largely to the ants, I believe it can

be shown that trophallaxis, originally developed as a mutual trophic relation between the mother insect and her larval brood, has expanded with the growth of the colony like an ever-widening vortex till it involves, first, all the adults as well as the brood and therefore the entire colony; second, a great number of species of alien insects that have managed to get a foothold in the nest as scavengers, *i. e.*, other species of ants (social parasitism); fourth, alien insects, predators or parasites (symphily); third, alien social insects, that live outside the nest and are "milked" by the ants (trophobiosis), and, fifth, certain plants which are visited or sometimes partly inhabited by the ants (phytophily). In other words the ants, have drawn their living environment, so far as this was possible, into a trophic relationship, which, though imperfect or one-sided in the cases of trophobiosis and photophily, has nevertheless some of the peculiarities of trophallaxis. A brief sketch of each of these five expansions, indicated as annular areas in the accompanying diagram (Fig. 12), may not be out of place.

1. There is a very close resemblance between the behavior of adult ants towards one another and their behavior towards their young. The adults feed one another with regurgitated food or even with secretions as is the case with *Crematogaster (Physocrema) inflata*, an Indomalayan species, the workers of which have great sugar-glands in the back of the thorax. Many ants transport each other, and the transported ant assumes a quiescent, larval or pupal attitude. This is best seen in certain Ponerinæ, *e. g.*, in the species of *Lobopelta*, which carry their males under the body as if they were larvæ or pupæ. On such occasions the males keep their legs and antennæ in the pupal position. Moreover, when the food-supply of the colony is cut off ants often devour other ants of the colony as if they were larvæ or pupæ. The largest workers (soldiers) are eliminated first, either because they represent more stored food or because their continued life in the colony constitutes a greater drain on the food resources, or for both reasons. Some years ago I recorded an instance of this behavior in an Arizona ant, which I called *Pheidole militicida*, because it regularly kills and eats all the large-headed soldiers in the colony during the winter when the food supply is very limited. In artificial nests of *Camponotus*, which has poly-

morphic workers, a similar elimination of the largest individuals may be observed when the colony is left long without food.

2. Among myrmecophiles and termitophiles Wasmann has shown that there are certain species (symphiles) that have trophallactic re-

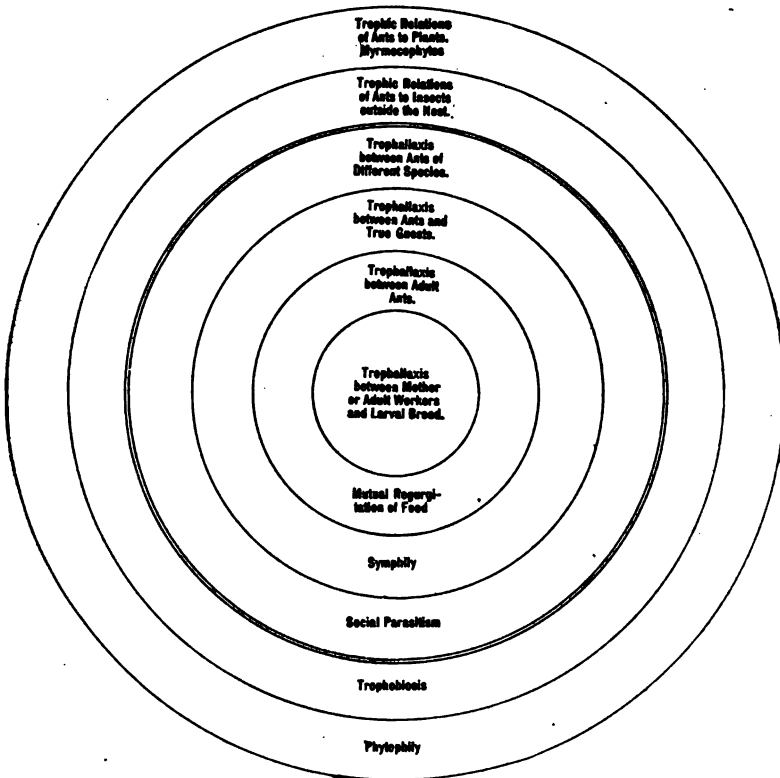


FIG. 12 Diagram to illustrate the expansions of the trophallactic and trophic relationships within and outside the ant colony. The confines of the nest are indicated by the double line.

lations with their hosts. Among ants especially these relations are so intimate that the symphiles may be regarded as integral members of the colony. The adult Lomeschusine beetles, *e. g.*, are not only fed and licked, but their young are treated as if they were ant larvæ, owing to the presence of trichome glands ("external exudate organs" of Wasmann) in the former and fatty, or internal exudatoria in the latter.

3. The various parasitic ants, of which a number of species have come to light within recent years and have been described by Wasmann, Donisthorpe, Emery, myself and others, can be shown to have established trophallactic relations with their host species. One of the most instructive is *Leptothorax emersoni* which lives with *Myrmica canadensis*. I have described its habits and those of one of its subspecies in three of my former papers (1901, 1903, 1907).

4. The relations of ants to plant-lice and other Homoptera and to the larvæ of Lepidoptera outside the nest are, as I have said, incompletely trophallactic, since these insects are not fed, though they may be defended by the ants. The Homoptera are not fed probably for the simple reason that their mouthparts are so peculiarly specialized for piercing plant-tissues and sucking their juices, and the Lepidopteron larvæ have, as a rule, no occasion to abandon their leaf diet. There are, however, several cases in which both caterpillars and Homoptera have entered into more intimate association with the ants. Many of the root aphids and coccids and their eggs are collected and kept by the ants in their nests, at least during certain seasons of the year. Two of the caterpillars that have acquired closer relations with the ants are so instructive, as illustrating one of the ways in which the myrmecophilous habit has been developed, that they merit more detailed description.

F. P. Dodd (1912) found that the first-stage larva of a small gray Queensland moth, *Cyclotorna monocentra*, is ectoparasitic on a Jassid Homopteron which feeds on certain trees and is attended and "milked" by an ant of the genus *Iridomyrmex*. The ant carries the parasite but not the Jassid into its nest. There the former spins a temporary cocoon and later emerges from it as a peculiar, flat, bright red (symphilic color), second stage larva, with two long tails. In this stage it subsists "solely on the ant grubs by sucking out their juices," but as in the case of *Lomechusa* in the nests of the European *Formica sanguinea*, the ant is partially recompensed for the loss of its brood. Dodd says:

Reference has been made to the caterpillars raising their terminal segments, even the small ones from the cocoons doing so. This was quite sufficient to warrant investigation. Consequently at various times I have placed them with ants and grubs under glass, in order that they could be seen to advantage and without risk of disturbance. When the anal parts are pro-

truded, an ant generally soon becomes aware of the fact and will be seen to pay these great attention. I soon noticed that a liquid, often perfectly transparent (it looks so on the blue-green ground, probably was pale bluish), is emitted, and that it is greedily drunk up by the ants. Over and over again, with and without a lens, I have seen this issue, and the ants speedily absorb it. Some ants, perhaps hungry or more enterprising than others, would take in a supply from a second caterpillar. If an ant is not satisfied with the quantity given out, she deliberately seizes the protruding parts and gives them a gentle nip, the mandibles can plainly be seen to press upon the juicy flesh; if the hint is not immediately acted upon a more vigorous squeeze is given, and the tails may be gripped and pressed. This is very comical, the ant's meaning is unmistakable and the caterpillar so thoroughly understands it, too, for a second hint never fails. This liquid, though frequently quite clear, is often mixed with yellowish matter, and at times some jelly-like substance is extruded; the latter the ants do not care about, for after the moisture is licked up this is in their way, and if they have not been imprisoned too long, will seize and tug at it until it comes off, and carry it to a spot set apart for waste matter, such as their own pellets and pupal skins, etc., are kept in.

Dodd also observed the ants licking and cleaning the caterpillar and the caterpillar cleaning the ants! When mature the caterpillar leaves the nest, travels to the nearest tree in company with the foraging ants, spins its cocoon in a crevice of the bark and pupates. In about twenty days the moth emerges.¹⁰

The second case is the caterpillar of *Lycana orion*, which has been recently studied by Chapman (1916, 1916a) and Frohawk (1916) in England. The butterfly lays its eggs on thyme and other plants. On these the larva feeds, and is often attended by ants as it possesses a honey-gland like many other larval *Lycænids*. When it has reached the third, or last moult it crawls down to the ground and on encountering a foraging worker of *Myrmica lævinodis* or *scabrinodis* hunches up the anterior segments of its body in a singular manner. . Frohawk interprets this behavior as a "signal" which induces the ant to seize the caterpillar and carry it into the nest.

¹⁰ When I was in Queensland Dodd generously gave me a fine series of all the stages of this extraordinary insect, together with specimens of its host ant. The latter, which I had previously found regularly nesting in the superficial portions of large, flat termitaria at Koah and Townsville, is not, as Dodd states in his paper, *Iridomyrmex purpureus* Smith (= *detectus* Smith), but *I. sanguineus* Forel. It is smaller and paler than *detectus*, but every bit as fierce and aggressive.

The individual ant which first finds the larva is always the one to carry it off. Although during its attendance several other ants may find the larva and stay by it a short time, and even milk it, they soon leave it to its original attendant, who apparently informs them that their services are not needed. [1] Whether the ant signals to the larva for it to prepare itself for transit, or the larva gives the signal that it is ready to be taken, seems doubtful; but from what we have seen both Capt. Purefoy and I are inclined to think that the larva gives the signal. No. 3 larva alluded to hunched itself both the second and third time while the ant was about an inch away and facing an opposite direction, and at the fourth hunching up the ant was standing over the larva ready for the signal, and when this was given it was quickly seized and carried.

Chapman observed that after the caterpillar was taken into the nest it fed on the *Myrmica* larvæ. During this period of its life it was not seen to yield the secretion of its honey-gland but was treated by the ants as what Wasmann would call an indifferently tolerated guest, or synœkete.

5. The fifth expansion of trophallaxis, namely the acquisition of trophic relations with the myrmecophytes, or plants possessing extra-floral nectaries or food-bodies, is also imperfect like ordinary trophobiosis, since the ants merely obtain nutriment from the plants and possibly afford them some protection. The nectar and other plant-foods are for the purposes of the ants merely so many exudates like the excrement of the Homoptera (honey-dew) and the sweet secretions of the Lycænid caterpillars which feed on the foliage.

As the foregoing study of trophallaxis has an important bearing on Wasmann's and Holmgren's interpretation of symphily it will be advisable to consider their views in greater detail. Wasmann has elaborated his ideas in regard to the origin and meaning of symphily in several papers, but as an article published in 1910 embodies his mature and apparently final contentions, his earlier publications need not be drawn into the discussion. Having found that particular symphiles live only with particular host ants and termites, he concludes, first, that the latter have during their phylogeny acquired particular symphilic instincts as differentiations or modifications of their original nursing and adoptive instincts, and second, that the true ant and termite guests have been developed by these symphilic instincts through a process called "amical selection," which he

likens to the conscious artificial selection employed by man in perfecting the numerous, often bizarre varieties among his domesticated animals and plants. Escherich (1898, 1902, 1911), Schimmer (1909, 1910) and I (1910) have never accepted this view, and I am still unable to see that Wasmann has successfully disposed of our arguments. The whole matter comes down to the answers to two questions: Do ants and termites possess special symphilic instincts? and: Is the assumption of amical selection necessary to account for the facts? In my opinion both questions are to be answered in the negative.

It is unnecessary to consider all the various symphilæ which Wasmann has so long and so carefully studied. A brief account of *Lomechusa strumosa*, his chief battle-horse and according to his own statement one of the most typical of symphilæ, will suffice. This is admittedly a predatory parasite in the colonies of *Formica sanguinea*. Its larvæ devour the ant larvæ and the adult beetles are fed and licked by the ants. The fat tissue of the larva probably supplies the ants with an agreeable exudate and the adults certainly furnish an agreeable secretion from their abdominal trichome glands. When the larvæ, which are evidently treated as if they were ant larvæ, mature, they are buried in the soil, just as the ant-larvæ are buried, in order that they may pupate. The pupæ are also unearthed like the ant pupæ, after they have spun their cocoons, but this treatment is fatal to the parasites and only those that have been forgotten and left in the soil are able to develop into beetles. Often the greater part of the ant brood is destroyed by the *Lomechusa* larvæ, but in some colonies, by a process which Wasmann has never adequately explained, many of the larvæ develop into pseudogynes, or forms intermediate between workers and females. These pathological individuals are unable to perform the functions of either of the castes which they imperfectly represent. This is in its essential outlines the history of *Lomechusa*. Now Wasmann believes that *Formica sanguinea* has acquired during its phylogeny a special symphilic instinct which impels it to foster *Lomechusa* to the detriment of the colonies and therefore to the detriment of the species, and regards the case as furnishing a splendid argument against natural selection and an incontestible proof of the existence

of amical selection. The same reasoning is, of course, made to apply, *mutatis mutandis*, to *Claviger testaceus* which lives with *Lasius flavus*, the Paussids which live with different species of *Pheidole*, the physogastric Staphylinids which live with various termites, etc. The bizarre structures of these symphiles, such as the antennæ of Clavigerids and Paussids, are compared with the deformities of some breeds of domestic animals and are supposed to have arisen and to have been perfected in an analogous manner. The analogy, as conceived by Wasmann, is indeed so close that it is hard to see why the term amical selection should have been introduced for what would seem to be after all only another case of Darwin's artificial selection though performed by ants instead of men.

The argument looks plausible till we examine it more critically. When we ask how the particular symphilic instinct to foster *Lomechusa* became established *i. e.*, hereditary, in *sanguinea*, we see that Wasmann has taken a great deal for granted. Of course, we really know nothing about the phylogeny of *sanguinea* in its relation to *Lomechusa*. The *sanguinea* queen and her fertile female offspring in colonies that are old enough to be infested by the beetle, pay no particular attention to the parasite and could therefore acquire such an instinct as Wasmann postulates only by inspiration. The workers, which do look after the beetles, rarely reproduce and probably never reproduce in infested colonies and would therefore not be in a position to transmit even if they acquired such an instinct. And as the *sanguinea* brood is either largely devoured or converted into infertile pseudogynes, so that the whole colony tends to die out, we have anything but a favorable environment for engendering and transmitting an instinct so specialized as to be concerned with a particular symphile. Furthermore, *Lomechusa* is a very sporadic parasite. It may be abundant in certain regions, as in certain parts of Holland, where Wasmann has worked and at St. Moritz, in the Upper Engadin of Switzerland where I once found it and its larvæ in considerable numbers, but there are many regions in which the *sanguinea* colonies are entirely free from the pest and hence in a flourishing condition and one most favorable to the survival of the species. Wasmann has not shown that *Lomechusa* introduced into

the colonies of such regions is treated with any less consideration than in young, previously uninfested colonies in regions where the parasite is common. As *Lomechusa* is very rare in England, the experiment could be readily performed by shipping a lot of the beetles from the continent to my friend Donisthorpe, with the request that he introduce them to the British *sanguinea*. I am willing to wager that even if they came from Germany they would be hospitably licked and fed by the ants of Albion. Wasmann might, however, contend that *Lomechusa* was once a universal *sanguinea* parasite or, at any rate, much more abundant and more uniformly distributed than at present, but if this had been the case how could *sanguinea* have survived, if the ravages of the parasite are as great as he asserts, especially when we consider that *sanguinea* is itself a parasite on another ant, *Formica fusca*, and is therefore dependent on a host?

The perusal of Wasmann's papers leaves me with the impression that he is bent on showing that symphily is something biologically unique and that for every peculiarity in ant behavior we are bound to postulate a specific instinct. If three of my maiden aunts are fond of pets and prefer cats, parrots and monkeys, respectively, I am not greatly enlightened when the family physician takes me aside and informs me sententiously that my aunt Eliza undoubtedly has an ælurophilous, my aunt Mary a psittacophilous and my aunt Jane a pithecophilous instinct, and that the possession of these instincts satisfactorily explains their behavior. It is only too apparent that the physician has merely called the stimuli that severally affect my aunts by Greek names *plus* a suffix indicating "fondness," assumed their existence as entities in my aunts' minds and naïvely drawn them forth as "explanations." It is high time that such scholastic methods of conducting biological inquiries were abandoned. *Entia non sunt multiplicanda præter necessitatem* in the study of animal behavior as in other fields of research.

The observations recorded in the opening pages of this paper seem to me to constitute the most formidable argument against the existence of special symphilic instincts, for in the first place, if in the social insects the relations between parent and offspring or between the nursing workers and the offspring of the fertile females

is trophallactic, it is clearly essentially the same as the relation between host and symphile. It becomes unnecessary, therefore, to assume that in the ants and termites the primitive nursing instinct, which is a mutual feeding, has been specialized or modified during the phylogeny in adaptation to particular symphiles. Slight ontogenetic modifications, well within the limits of the plastic, or "intelligent" behavior of the ants, as responses to the specific organization of the symphiles, seem amply sufficient to account for the phenomena.

In the second place, trophallaxis is, of course, traceable to a mutualistic hunger, or "exudate hunger" as Holmgren calls it, and therefore to an appetite, in the sense in which this term is employed by English psychologists. In view of the fact that psychologists have universally regarded the appetites as very primitive and fundamental it is rather strange that they have received so little attention from the animal behaviorist. Very recently, however, Drever (1917) and Craig (1918) have emphasized their importance in connection with instinct in two valuable contributions. Drever regards the appetites as very simple or primitive instincts or "as representing an earlier stage of conscious life, which in the human being and the higher animals, is overlaid by the stage to which the development of the specific 'instinct' tendencies belong." He enumerates the hunger, thirst and sex appetites, the appetite for sleep or rest, for exercise or activity, "nausea," or "primitive disgust" and James' "instinct of personal isolation." Craig's contribution is particularly interesting because he reaches his conclusions from a study of birds (doves) and deals with the matter more thoroughly. According to him the appetites and aversions are constituents of the instincts. "Each instinct involves an element of appetite, or aversion, or both." Perhaps his view is not essentially different from Drever's, since the most typical appetites, those of hunger and sex, represent the basic reactions of organisms, and what are ordinarily called "instincts," *i. e.*, the chain-reflexes, or more elaborate mechanized behavior of animals, are evidently later and superposed activities that, so to speak, adopt the general movement or pattern of expression characteristic of the appetites. Craig, in fact, resolves the behavior of animals into cycles which run their course according to

the appetite or aversion schema. He evidently regards sexual behavior as the most typical expression of appetite. I should regard hunger as being certainly from a biological point of view the more primitive.¹¹

If we regard symphily and trophallaxis as expressions of essentially the same instinct with pronounced appetitive constituent or pattern, we can readily understand how Wasmann was led astray by the behavior of *sanguinea* towards *Lomechusa*, for the appetites are notoriously prone to perversion. In fact, Escherich's comparison of the appetite of *sanguinea* for the secretions of the beetle with alcoholism is not altogether inept. I should prefer to compare the ant's behavior with that of a cat presented with a sprig of catnip or of a leopard presented with a ball of paper sprinkled with oil of bergamot. If the secretions of the larval and adult *Lomechusa* have an analogous influence on their hosts, as is very probable, the apparently anomalous behavior of the latter would be readily understood. It would certainly be no more surprising than that my hypothetical maiden aunts prefer to have their bed-linen scented with lavender or that some of my bachelor friends prefer Havana cigars and cannot be persuaded to smoke the "domestic" variety.

If the objection be raised that I overlook the fact that the relation of *sanguinea* to *Lomechusa* is one of host to parasite, whereas that between the queen ant and her brood is one of parent to off-

¹¹ I find myself therefore in closer agreement with Jung than with Freud. The former's term "libido" seems to be practically synonymous with "appetite" in its general sense, as *e. g.*, in the following very suggestive passage (1916, p. 149): "We see the libido in the stage of childhood almost wholly occupied in the instinct of nutrition, which takes care of the upbuilding of the body. With the development of the body there are successively opened new spheres of application for the libido. The last sphere of application, and surpassing all the others in its functional significance, is sexuality, which seems at first almost bound up with the function of nutrition. (Compare with this the influence of procreation on the conditions of nutrition in lower animals and plants.) In the territory of sexuality, the libido wins that formation, the enormous importance of which has justified us in the use of the term libido in general. Here the libido appears very properly as an impulse to procreation and almost in the form of an undifferentiated sexual primal libido, as an energy of growth, which clearly forces the individual towards division, budding, etc. (The clearest distinction between the two forms of libido is to be found among those animals in whom the stage of nutrition is separated from the sexual stage by a chrysalis stage.)"

spring, I would reply that from a general biological point of view the resemblances between the two cases are still fundamental and suggestive. This has been shown by Giard in one of his interesting papers (1905, 1911). He says:

Comparative ethology permits us to go further and shows us in the clearest manner that the relations between the parent organism and its progeny are in principle absolutely the same as those which exist between a parasitized animal and its parasite and that after a period of unstable equilibrium, in which one or the other of the two organisms in contact finds itself injured to the profit of its associate, there is a tendency to establish a definitive status of mutual equilibrium in which the two partners find in their association an advantage in the struggle against the *ensemble* of common causes of destruction, both cosmic and bionomic.

A partial attainment of the equilibrium mentioned by Giard, both in the nursing relation of ants and that of *sanguinea* to *Lomechusa* is brought about by mutual feeding. In neither case is the exchange of food between the two parties quantitatively equal, but the exudates as stimuli, in all probability make up in quality or intensity for what they lack in quantity.

This brings us back to Wasmann's amical selection which still remains to be considered. It has often been remarked that the symphiles are strangely like our domestic animals in that they live in a social environment where they are protected from enemies and abundantly fed. In the case of the domestic animals Darwin long ago showed that such an environment favors the production of extraordinary variations, and Pearson (1897) and Trotter (1916) agree that when organisms unite to form larger biological units such as the Metazoan body, herds, colonies and societies, the individuals though necessarily limited in their evolution along particular lines nevertheless in other respects escape from the stabilizing influence of natural selection and exhibit unusual freedom of development and specialization. Both the domestic animals and the symphiles which really become integral members of the insect societies in which they are permitted to live, show this freedom in the development of unusual structural and color characters, as we see in albinos, peculiar breeds of fowl, pigeons and dogs, Paussids and Clavigerids with monstrous antennæ, ant-chalcids like *Kapala* and *Isomeralia*, with huge thoracic spines, etc. Similar phenomena are common in many

ecto- and entoparasites which are intimately associated with their hosts (*e. g.*, *Sacculina*, many Copepods, Isopods, tapeworms, etc.). The origin of these strange characters is evidently spontaneous, or mutational and dependent on the favorable conditions under which they arise. In the case of the domestic animals we know that the unusual characters are being continuously and rapidly perfected and established by man's selective activity. It does not follow, however, that the analogous developments of symphiles are the outcome of a similar activity on the part of the ants and termites. The resemblance of the aberrant characters of symphiles to "hypertelic" structures in many other insects has been noticed by Dahl. That the phenomena in both cases are due to the same cause, *i. e.*, the relaxation or suppression of natural selection, is much more probable than Wasmann's contention that the ants take the same interest in breeding Paussids and Clavigerids with extraordinary antennæ that we do in breeding lop-eared rabbits and fan-tail pigeons. Nor is there any evidence that even the biologically useful characters of the symphiles, namely their trichome glands and exudate tissues, are engendered or perfected by amical selection. The truly amazing cases of convergent or parallel development of these structures in symphiles belonging to the most diverse genera is, in all probability, attributable to the adaptive activities of the symphiles themselves, just as we attribute the convergent development of hooks, suckers, hermaphroditism, blindness, etc., in entoparasitic worms or aptery in ectoparasitic insects, such as lice, fleas, Polycetenids, Nycteribids, etc., to the parasites themselves and not to specifically selective efforts on the part of the host organisms.

Holmgren accepts Wasmann's amical selection and carries it a step further in his contention that it accounts for the development of the various castes in the termite colony. He says (1909, p. 200) :

If now the above described connection between feeding and exudate secretion holds good, so that the quantity of exudate secretion determines the kind of feeding, it would seem to be self-evident that the exudate secretion is intimately connected with the development of castes, for Grassi and Sandias have shown that feeding is probably to be regarded as a factor in caste development. And if, therefore, the exudate secretion is the cause of feeding we must regard it as the cause of the differentiation of the various castes.

That this opinion is no longer tenable, at least in the form in which it is stated, is shown by the observations of Bugnion (1912), who has proved that the soldier and worker castes of *Eutermes* are determined in the egg, and the observations of Miss Thompson (1917), who has been able to distinguish the sexual from the sterile castes of *Leucotermes flavipes* at the time of hatching. Holmgren's thesis could be accepted only on the assumption that the effects of feeding had been carried back during the long phylogeny of the termites into the embryonic stages. Incidentally it may be said that his other statement in regard to the development of the complemental or neotenic males and females in the termite colony refer, not to the development of castes, but to the ontogenetic growth of the exudate tissues, a process which is exhibited in the most extraordinary manner during the imaginal life of the true queens of many species.

In conclusion it may be interesting to note in connection with the development of the social habit of insects from a trophallactic relation between parent and progeny, that the social or gregarious instinct in man has also been regarded by some authors as an appetite. Drever (1917) cites the early British philosopher Hutcheson ("Nature and Conduct of the Passions," Sect. 4, 1728) as classifying the gregarious instinct among the appetites, and referring to McDougal's interesting comments on gregariousness (1910), he says (p. 184):

There is in the instinct itself something which suggests such a view [as McDougal's], something which might even lead the psychologist to maintain that it belongs to the "Appetite" group in our system of classification, an opinion to which Galton's description [of the wild ox of Damaraland which cannot endure even a momentary severance from the herd] would lend some support. There is indeed something primordial about the whole experience involved in the operation of the gregarious instinct.

The fact that higher gregarious and social animals are satisfied as long as they are with their fellows but become uneasy when isolated is certainly very suggestive of the appetitive type of behavior.¹² In

¹² As Trotter says (1916). "In interpreting into mental terms the consequences of gregariousness, we may conveniently begin with the simplest. The conscious individual will feel an unanalyzable primary sense of comfort in the actual presence of his fellows, and a similar sense of discomfort in their absence. It will be obvious truth to him that it is not good for the man to be alone. Loneliness will be a real terror, insurmountable by reason."

this connection some of Le Dantec's recent writings are of considerable interest. In a footnote (p. 288) at the end of "Les Influences Ancestrales" (1917) he asks:

Does maternal love, which has assumed such great moral significance in the human species, originate among the females of the Mammalia as the desire (*souci*) to rid themselves of their milk?

A similar tendency to show that the social relation in man has an egoistic instead of an altruistic foundation is even more forcibly displayed in his startling not to say shocking, volume entitled "L'Égoisme Seule Base de Toute Société" (1916).¹³

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¹³ Since the foregoing paragraphs were written I have found two quotations from Charles Bonnet's "Contemplation de la Nature," which are the more remarkable because they were published in 1764. On p. 213 he says: "In order the better to insure the well-being of their progeny, would not Nature have engaged the affection of the mothers in such a manner that the young would become for them a source of agreeable sensations and material usefulness? Certain facts seem to confirm this conjecture. . . . The mammæ have been constructed with such art that the sucking and pressure exerted by the young excite the nerves which impart to these organs a delicate disturbance or soft commotion accompanied by a feeling of pleasure. This pleasure sustains the natural affection of the mother, if indeed it be not one of its principal causes. The same may be said of the action of licking, which is reciprocal. Finally, mothers are sometimes incommoded by the abundance of their milk; the young relieve them by sucking." The second quotation (p. 272) is even more astonishing in its bearing on the conditions in the social insects: "The neuters [of bees] have no sex and do not reproduce. How can we suppose that they have the same affection for the offspring of their queen as the mothers of other animals? They behave nevertheless in the same manner under the same circumstances. If, therefore, Nature has known how to insure the attachment of mothers by the agreeable sensations derived from their offspring or by the services they render, it would certainly seem that she must employ much the same means in the case of the worker bees and that she has placed in the young a secret source of delectable sensations which attaches them to the workers and induces them to disgorge into the cells the kind of porridge with which the young are nourished." These quotations are from a work entitled "La Psychologie Animale de Charles Bonnet" published in 1909 in Geneva by Ed. Claparède who cites them and the work of Giard in support of his views on the reciprocal relations of the mother to her offspring.

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DEVELOPMENT OF MAGNETIC SUSCEPTIBILITY IN MANGANESE STEEL BY PROLONGED HEAT TREATMENT.

By CHARLES F. BRUSH.

(Read April 19, 1918.)

During the past three years I have had the honor of presenting several papers on "Spontaneous generation of heat in recently hardened steel,"¹ showing that all the specimens treated spontaneously generated heat in easily measurable quantity after hardening by quenching in water at various temperatures above the critical temperature of decalescence. Carbon tool steel, "high-speed" tungsten-chromium steel, and several specimens of nickel-chromium steel were tested. In all cases the generation of heat was most pronounced immediately after quenching and diminished rapidly, though it continued observable a week or more. Generation of heat was always conditional on true hardening, by quenching at a temperature above the critical point, except in the case of one of the nickel-chromium specimens. Here moderate, but unequivocal, generation of heat followed quenching at a temperature just *below* the critical point, reached by *falling* slowly from a higher temperature through full recalescence. While true hardening could not have occurred, yet there was a well-marked "stiffening" or incipient hardening of the metal as shown by subsequent hardness tests. When, however, the same steel, after annealing, was slowly *raised* to the same temperature (but not above) and quenched, no generation of heat followed. In this connection another interesting phenomenon developed as follows: When the same lot of nickel-chromium steel, after annealing, was quenched at several successively higher (rising) temperatures, but all below the critical temperature,

¹ *Proc. Am. Phil. Soc.*, Vol. LIV., No. 217, May-July, 1915. *Phys. Review*, N. S., Vol. IX., No. 3, March, 1917. *Proc. Royal Soc.*, Series A, Vol. 93, No. A, 649, Apl. 2, 1917. Joint paper with Sir Robert Hadfield. *Proc. Am. Phil. Soc.*, Vol. LIV., No. 4, 1917.

each quenching was followed by a small but distinct *absorption* of heat.

The phenomena above outlined appear to be new, and have aroused the interest of some eminent metallurgists, among others Sir Robert A. Hadfield, who kindly furnished all the specimens of nickel-chromium steel employed, and to whom I am greatly indebted for joining in some of the later work, and incidentally confirming the most important of my findings with different apparatus of his own design.

The foregoing outline of former work is introduced here because it underlies, and is closely associated with, the subject matter of the present paper.

Sir Robert Hadfield long ago suggested that interesting results might follow similar experiments with manganese alloy-steel (with which his name is so intimately connected).

As is well known, this remarkable steel is exceedingly tough, and difficult to work with machine tools though not hard; its softest and toughest condition is brought about by water-quenching at a high temperature, after which it is almost completely non-magnetic; it has no critical temperature, and hence cannot be hardened in the ordinary sense; when heated a long time at a moderate temperature it becomes magnetic, loses much of its tensile strength, and all its toughness, and becomes brittle and considerably harder.

For the purposes of the following experiments Sir Robert Hadfield sent me 19 numbered bars of his manganese steel, each 6 inches long and $\frac{1}{2}$ inch in diameter (round), all cut from the same long bar and ground to size after treatment.

Following is his specification:

Analysis.—C, 1.18 per cent.; Si, .14 per cent.; Mn, 12.29 per cent.

Bars 1 to 6, As forged. Non-magnetic.

Bars 7 to 12, Toughened by water-quenching at 995° C. Non-magnetic.

Bars 13 to 18, Toughened as above, then reheated to 500° and kept at that temperature 63 hours. Magnetic.

Bar 19, Treated like 13 to 18, then reheated to 995° and water-quenched. Non-magnetic.

I carefully tested one bar of each description for scleroscope hardness, with following results:

Bar No. 1 (as forged). Hardness 37.3.

Bar No. 7 (toughened). Hardness 28.5.

Bar No. 15 (toughened, reheated). Hardness 51.6.

Bar No. 19 (toughened, reheated, retoughened). Hardness 39.

Each of the above hardness numbers (and those to follow) is the mean of at least ten consistent measurements made on the carefully ground, horizontal end surface of the bar, a fresh spot being used for each measurement.

I subsequently heated bar No. 13 to 1074° and cooled (annealed) in the furnace. Its hardness, which presumably had been about 51.6 like its companion No. 15, was then 28.8, and it was non-magnetic; seeming to show that quenching at high temperature, and annealing from a still higher temperature, gives the same hardness and non-magnetic condition whatever previous treatment may have been. The hardness of bar No. 19 seems to contradict this conclusion, in respect of hardness, but it was quenched at a very considerably lower temperature.

In the following experiments ten of the 6-inch bars of manganese steel were used, so as to approximately equal in weight the twelve 5-inch bars of other steels employed in former experiments.

First quenching: Bars 1 to 5 and 7 to 11 (10 in all) were heated in an electric muffle furnace to 1013° C. and quenched in water. This treatment was followed by no appreciable generation or absorption of heat when tested in the calorimeter employed in former experiments and described in the earlier papers referred to.

Hardness was now: Bar No. 1, 30; Bar No. 7, 28.3, showing that the first lot "as forged" and the second lot "toughened" were brought to substantially the same "toughened" condition.

Second quenching: The ten bars were again heated to 1013° , allowed to cool in the furnace to 800° and quenched. Again there followed no appreciable generation or absorption of heat.

Hardness was now: Bar No. 1, 27.6; Bar No. 7, 26.3.

Third quenching: The bars were heated to 818° , allowed to cool in the furnace to 607° , and quenched. There was no subsequent generation or absorption of heat.

Hardness was: Bar No. 1, 26.3; Bar No. 7, 26.6.

The ten bars were next heated slowly to 645° and allowed to cool slowly in the furnace to room temperature.

Hardness was: Bar No. 1, 26.5; Bar No. 7, 25.9.

All the bars were now very moderately magnetic, though in their softest condition.

The foregoing quenching temperatures were *falling* ones. The following quenching temperature was a *rising* one, from the annealed condition last described.

Fourth quenching: The bars were heated slowly to 615° and quenched.

Hardness was now: Bar No. 1, 38; Bar No. 7, 30.3.

Notwithstanding this considerable increase of hardness, there followed no appreciable generation or absorption of heat. The bars remained very moderately magnetic.

The results of the foregoing experiments make it highly probable that no spontaneous generation or absorption of heat can be brought about by quenching this manganese steel at any temperature, rising or falling, while in its normal, useful non-magnetic condition. But it was thought worth while to make further experiments with the steel in its magnetic condition and, incidentally, to study the development of this magnetic condition during the prolonged moderate heating necessary to bring it about. The latter study has proved so interesting that I have pursued it to considerable length and made it the titular subject of this paper.

The apparatus employed in the following study consists, in part, of a vertical cylindrical electric furnace heated by small spirals of "nichrome" wire carrying alternating current regulated by a rheostat. The heating spirals are so disposed as not to produce any magnetic field inside or outside the furnace. Instead of the usual sheet-iron casing, this furnace is cased with sheet brass slotted longitudinally to prevent induction currents in it when the external magnetizing solenoid is excited. The furnace is surrounded by a solenoid 16 inches inside, and 20 inches outside diameter, and 4 inches long (high), consisting of 860 turns of No. 12 insulated copper wire wound in two equal coils adapted to be placed in series or parallel relation by means of a suitable switch. The axes of the

furnace and solenoid are coincident. The solenoid is excited by current from a 65-volt storage battery, controlled by a rheostat, and the circuit is closed and opened by a switch which breaks simultaneously at three points in series, so as to avoid the destructive arc which would occur at a single break. An ammeter and reversing switch are included in the line.

A single turn of asbestos-insulated platinum wire is located in the furnace, and the ends of this loop are connected by a twisted cable with a ballistic mirror-galvanometer of 600 ohms' resistance.

When the solenoid circuit is closed, a brief electric current is induced in the platinum loop in the furnace and causes a minimum swing of the galvanometer scale easily read with considerable precision.

When a bundle of ordinary steel or iron bars is placed within the platinum loop the galvanometer deflection is, of course, many times greater, and is fairly proportional to their magnetic susceptibility, after deducting the minimum deflection due to the platinum loop alone, and when the excitation of the solenoid is not too small or too great. In the following experiments with the manganese steel, 9 amperes was found to be suitable exciting current with the solenoid coils in series. Small variations of exciting current were reduced to this value in computing results. Residual magnetism was measured by the usual method of reversals, and allowed for.

The above described apparatus was originally designed and constructed for a rough study of the magnetic properties of metals and alloys at temperatures up to and above their melting points, and has proved very useful. A high-temperature furnace with slotted brass casing is included in the general outfit.

Preparatory to the following study of magnetic susceptibility of the manganese steel brought about by prolonged heating, ten half inch round bars, 6" long, of Swedish charcoal iron were placed within the platinum loop in the furnace, and the galvanometer deflection was repeatedly observed when the solenoid was excited by various amounts of current. Nine amperes was found to give conveniently large deflection, which was closely proportional to the current through a wide range about this value. This condition was also found approximately true when the manganese steel bars, made

magnetic by heating, were subsequently substituted for the charcoal iron.

In the following experiments galvanometer deflection, less that amount due to the platinum loop alone, is taken as the measure of magnetic susceptibility, and the susceptibility of the Swedish iron is used as a standard and assigned a value of 100. All other values are reduced to and expressed in terms of this standard.

As a preparatory measure, the ten bars of manganese steel were brought to their softest and toughest condition by quenching at 1000° .

Hardness was: Bar No. 1, 26.7; Bar No. 7, 25.8.

All the bars were quite free from any trace of magnetism.

The bars were next placed within the platinum loop in the electric furnace and heated 170 hours to a temperature fluctuating between 505° and 525° . The growth of magnetic susceptibility is plotted in the curve shown in Fig. 1. There is no doubt that the

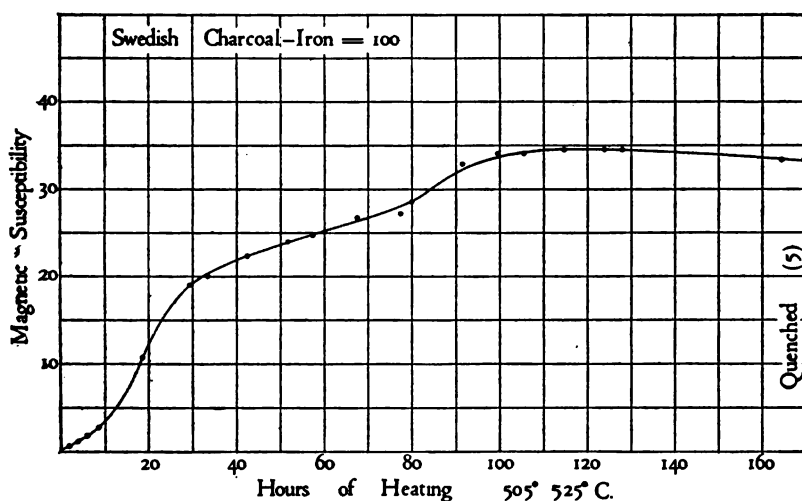


FIG. 1.

curve would have been smoother if the temperature had remained constant. It was intended to use about 515° temperature, and it was held near that value by the rheostat during the first few hours. Subsequent fluctuations were due to variations of voltage in the

alternating heating current. The higher temperatures usually occurred in the latter part of the night, and were always accompanied by more than average rise of susceptibility. But the large depression in the central part of the curve is thought to be due to some obscure cause, and not to temperature variation.

The entire absence of growth of susceptibility during the last 50 or more hours prompted the belief that the steel had reached a stable condition at the temperature of treatment, and led to the discontinuance of this experiment. Permanent magnetism, which had been considerable while susceptibility was rising, fell off very much during the last two or three days.

Fifth quenching: At the end of 170 hours the bars were quenched, after which they exhibited moderate, but typical and unequivocal generation of heat.

Hardness was: Bar No. 1, 48.1; Bar No. 7, 47.2.

This great increase of hardness (from 26.7 and 25.8 in the annealed condition) brought about by the long heating, doubtless accounts for the spontaneous generation of heat observed.

During the long heating the bars acquired a rather thick coating of black oxide which peeled off almost completely in quenching, leaving clean metal surface. The oxide was strongly magnetic; but its weight was so small, compared with the total weight of the bars, that it could not have affected, materially, the foregoing magnetic observations.

The bars were again placed in the furnace and heated to a higher temperature than before, fluctuating between 590° and 598° , for the first 90 hours (from 170 to 260 hours, reckoned from beginning of treatment).

The results of this procedure are plotted in the first curve of Fig. 2. It is seen that magnetic susceptibility started at a very considerably higher value than it had at the end of the previous treatment. The reason of this increase during the intervening few days, without heating, is not clear. It may have occurred at the moment of quenching; or, more likely, during the period of spontaneous heat generation which followed the quenching.

The curve shows a very regular, but steadily diminishing, growth

of susceptibility at this higher temperature, until it reaches nearly double the value it had at the end of the previous treatment.

Fig. 2 shows that at the 260-hour point of total treatment the temperature was quickly raised about 25° , *i. e.*, to 619° , and continued at that point about ten hours. This moderate rise in temperature brought about a sudden and very considerable fall in susceptibility, approaching stability at the end of the ten hours.

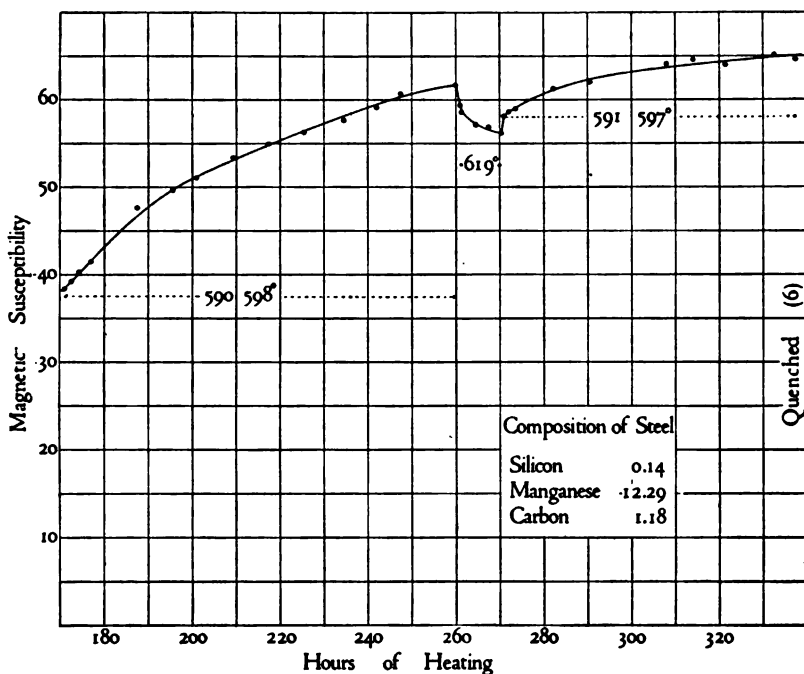


FIG. 2.

When the temperature was next quickly lowered to its former value and then continued to the end of the experiment, 175 hours (340 hours total), there was at first a sudden rise of susceptibility, followed by steady growth as before. All these changes are clearly shown in Fig. 2.

Great sensitiveness to temperature change is indicated at about 600° .

Sixth quenching: At the end of 344 hours, total, of treatment,

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the bars were again quenched. This was followed by very little, if any, spontaneous generation of heat.

Hardness was: Bar No. 1, 37.4; Bar No. 7, 36.2.

This shows a very considerable softening since the last quenching, notwithstanding the large increase of magnetic susceptibility. The softening may account for the absence of heat generation after the quenching.

The magnetic susceptibility of the cold quenched bars was almost the same (slightly lower) as before quenching.

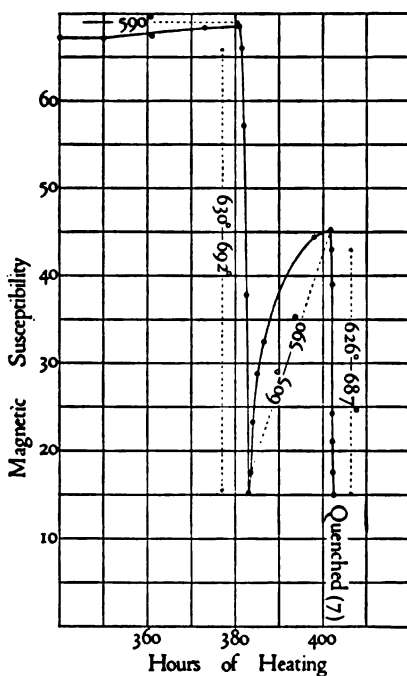


FIG. 3.

The ten bars were again heated, slowly this time, to 590° and held nearly at that temperature until the 381st hour of total treatment, as shown in Fig. 3. Susceptibility rose slightly, reaching its highest value, 68.5. As this is comparable with the susceptibility of ordinary steel, the manganese had apparently almost completely lost its influence.

At this stage it was thought that decalescence might possibly be brought about by cautiously raising the temperature, and the effect of doing so is shown in the great and nearly vertical drop in the susceptibility curve. The stations in this part of the curve represent observations at half-hour intervals, indicating two hours for the total drop, with the temperature steadily rising to the maximum of 692° .

It seemed clear that decalescence was not taking place, because loss of susceptibility was far too slow in time, and the maximum temperature reached was not sufficiently high. Probably the manganese was simply resuming its sway.

The temperature was next rapidly lowered to 605° – 590° , bringing on a rapid recovery of magnetic susceptibility, amounting to 30 points in 21 hours as shown.

Again the temperature was raised, but much more rapidly than before, resulting in a much steeper drop in the curve, the observation stations shown representing only five-minute intervals.

Seventh quenching: At the end of the curve shown in Fig. 3 the steel bars were quenched at 687° . Subsequently there was no trace of generation or absorption of heat. Hence it is virtually certain there had been no decalescence.

Hardness was: Bar No. 1, 42; Bar No. 7, 41.8.

Sir Robert Hadfield long ago assured me that the study of manganese steel is full of surprises for the investigator. I have experienced some of them, and hesitate at present to draw definite conclusions from the results of the experiments just described. The manner in which the manganese operates in completely obliterating the magnetic quality of seven times its weight of iron is, so far as I am aware, not yet known; and the instability of the alloy or, probably, mixture of alloys, in which the carbon present may play an important part, at about 600° temperature as herein shown, is most remarkable and promises a fertile field for future investigation.

I am contemplating the study of a similar ferro-manganese alloy free from carbon.

CLEVELAND, O.,
April, 1918.

PRELIMINARY NOTES ON SOME NEW SPECIES OF AGARICS.

By GEO. F. ATKINSON.

(Read April 19, 1918.)

***Amanita brunnescens* nov. sp.** Gregaria vel dispersgens, 8-15 cm. alta: pileo convexo dein expanso, fuligineo-brunneo, 4-9 cm. lato, subumbonato, in centro obscuriore, ad marginem pallidiore et frequenter brunneo virgato vel maculato, e calyptra volvæ floccoso squamoso, squamis albis vel pallido-ochraceis, interdum margine pilei albo, rare pileo albo, matura margine pilei interdum striatulo: lamellis leniter attigentibus, albis: sporis quaternis, albis, globosis, 8-10 μ : stipite albo, abrupte bulboso, floccoso-squamuloso, 4-10 mm. crasso: annulo amplo, membraneo, superiore, albo vel pallide albo, demum murino: bulbo stipitis 2-3 cm. crasso, margine bulbi limbo volvæ curto, acuto prædito. Stipite, bulbo, et interdum carne pilei, tactu brunnescens.

This is one of the most common species of *Amanita* in the eastern United States, and I have observed it for many years. It is usually interpreted as a dark brown form of *Amanita phalloides*. For a number of years I have regarded it as a distinct species. Typical *Amanita phalloides* which I have collected in France has been compared and confirms this opinion. The spores of typical *Am. phalloides* are subglobose to oboval or subellipsoid, and bruises do not change to a reddish brown color. The American plant being a different species may account for different results, obtained in chemical analyses, from those reported for the typical *Amanita phalloides* of Europe.

No. 24277, type, C. U. Herb., ground, woods, west of Cayuga Lake, near Ithaca, N. Y. July 30, 1917. Leva B. Walker collector.

***Amanita pachysperma* nov. sp.** Gregaria vel dispersgens, 4-5 cm. alta: pileo campanulato dein convexo, umbonato, 1.5-2 cm. lato, cinereo, e calyptra volvæ dense et minute squamuloso, margine ad umbonem striato, carne tenue: lamellis albis, ellipsoideo-ventricosis, basidiis abrupte clavatis, 35-45 \times 12-15 μ : sporis binis, subellipsoideo-obovalibus, 11-15 \times 8-10 μ , sed 20 \times 8, 18 \times 12, 12 \times 8, 11 \times 8, 10 \times 7, uniguttulatis: stipite albo, leniter bulboso, floccoso-squamuloso, 3-4 mm. crasso: annulo membraneo, albo, superiore et persistente: limbo volvæ libero, persistente.

In shape and color resembles *Amanita cinerea* Bres. (Fung. Trid. 1, 7, pl. 1, 1881), but spores larger, basidia two-spored, and striations on pileus more extended.

No. 3711, type, C. U. Herb., in sandy ground in woods, Blowing Rock, Watauga Co., N. C. Aug. 19–Sept. 19, 1899. G. F. Atkinson collector.

Hypholoma comatum nov. sp. Gregarium vel dispergens, 3–5 cm. altum: pileo ovali dein campanulato, albo, demum nigro-griseo et leniter striatulo, 0.5–1.5 cm. lato, adolescente radiatis hyphis dense prædito, dein sericeo-fibrilloso, margine appendiculato: lamellis stipite adnatis, ellipticis, cinereis dein cinereo-nigrescentibus: cystidiis solum in acie lamellarum, numerosis, clavato-ventricosis vel subcylindricis, membrana tenui, $40-55 \times 10-12 \mu$: sporis quaternis, anguste subellipsoideis, purpureo-brunneis vel purpureo-nigrescentibus, levibus, $12-14 \times 6-7 \mu$: stipite æquali, albo, bulbilloso, recto vel flexuoso, fibrilloso-squamoso, 1–1.5 mm. crasso.

No. 24195, type, C. U. Herb., on ground on humus and buried twigs, lawn by East Ave., Campus, Cornell University, Ithaca, N. Y. July 16, 1917. G. F. Atkinson collector.

Hypholoma confertissimum nov. sp. Dense cæspitosum, 8–12 cm. altum et 10–20 cm. latum: pileo ovali dein convexo, 1–3.5 cm. lato, hygrophano, pallide argillaceo, demum pallide ochroleuco vel pallide albo, in centro argillaceo et ruguloso, velo universali albo-floccoso, demum pileo fibrilloso-squamoso et appendiculato et pallide cinereo-brunneo maculato vel virgato: lamellis stipite adnato-adnexis, demum liberatis, ellipticis, confertissimis, cinereis dein purpureo-brunneis, acie alba: cystidiis in superficie et acie lamellarum subfusoides-ventricosis, $35-50 \times 11-14 \mu$: sporis quaternis, purpureo-brunneis, levibus, $5-7 \times 2.5-3 \mu$: stipite æquali, recto vel flexuoso, albo, cavo, albo-floccoso-squamoso, fragili, 3–5 mm. crasso, membrana mycelii oriente.

No. 25063, type, C. U. Herb., tufts of 50–100 individuals from dead roots or buried wood, in forest of mixed hard wood, Hoop Pole Ridge, west of Oakland, Md. Sept. 24, 1917. G. F. Atkinson collector. This species is related to *Hypoloma aggregatum* Peck, but differs in its smaller spores, different cystidia, yellow mat of mycelium, etc.

Lactarius nigroviolascens nov. sp. Dispergens, 5–6 cm. altus: pileo 3–5 cm. alto, convexo, incurvato, demum expanso et in centrum depresso, interdum umbonato, atro-brunneo, demum fulvo-olivaceo et in centro obscuriore, pruinoso et ruguloso: margine pilei demum

striato et crenato: lamellis stipite adnatis in lineis decurrentibus, subdistantibus, albis dein ochraceis et obscurioribus: sporis quaternis, subglobosis: echinulatis, $8-10\mu$: stipite æquali, pileo concolore, minute et densissime tomentuloso: lacte carneque dulci, albo, contactu aëris nigro-violascente.

No. 24257, type, C. U. Herb., ground, woods, Coy Glen near Ithaca, N. Y. July 25, 1917. Leva B. Walker collector. Related to *Lactarius fuliginosus*.

Lactarius villosozonatus nov. sp. Dispergens vel subcespitosus, 3–5 cm. altus: pileo 8–12 cm. lato, ochraceo vel ochroleuco, villosus, zonatus, convexus et depressus, demum infundibuliforme: margine pilei fortissime incurvato, demum expanso et prominenter crenato: lamellis stipite adnexis et sinuatis, angustis, subdistantibus: sporis subglobosis vel leniter elongatis, echinulatis, $8-10\mu$, vel $8-10 \times 10-12\mu$: stipite glabro, 1.5–3 cm. crasso: lacte ex hyalino brunnescente, tarde acri.

No. 20215, type, C. U. Herb., ground woods, Port Jefferson, L. I., N. Y. Aug. 26–Sept. 2, 1904. G. F. Atkinson collector.

Lepiota rhombospora nov. sp. Gregaria vel solitaria, 3–4 cm. alta: pileo convexo, 8–15 mm. lato, 1 cm. alto, adolescente ochraceo-fulvo, demum ochroleuco granuloso et squamuloso: squamulis cellis rotundatis vel obovatis vel pyriformibus præditis: lamellis stipite adnatis vel adnexis, sinuatis, ventricosis, argillaceis: cystidiis solum in acie lamellarum, lanceoideis, $24-32 \times 6-8\mu$: sporis quaternis, bilateralibus, albis, a fronte rhomboideis et utrimque acutiusculis, a latere inequilateralibus, levibus, $4-5 \times 3-4\mu$: stipite æquali, pileo concolore, granuloso et squamuloso.

Nos. 24323 and 24324, type, C. U. Herb., in edge of mixed woods, on leaf mold, by Stewart's Camp, Seventh Lake, Adirondack Mts. Aug. 16 and 21, 1917. F. C. Stewart collector.

Pholiota retiphylla nov. sp. Gregaria, 2–3 cm. alta: pileo lateritio vel vinaceo-cinnamomeo, 1–2.5 cm. lato, convexo dein expanso, sericeo-tomentosulo, margine incurvato, carne vinaceo tincta: lamellis stipite adnatis, leniter emarginatis, angustatis, confertissimis, vinaceo-rufis, superficie lamellarum venosa et reticulata: cystidiis nullis: sporis quaternis, subovalibus, levibus, rufo-luteis, $5.5-7 \times 4-4.5\mu$: stipite interdum bulboso, demum æquali, fibroso-striato, cavo, carne vinaceo-tincta 4–8 mm. crasso: annulo membranaceo, tenui, vinaceo.

No. 18540, type, C. U. Herb., on very rotten moss-covered log, woods, Malloryville moor between McLean and Cortland, N. Y. Aug. 18, 1904. H. S. Jackson and H. H. Whetzel collectors.

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Vol. LVII.

1918.

No. 5.

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THE GENUS GALERULA IN NORTH AMERICA.

By GEO. F. ATKINSON.

(Read April 19, 1918.)

*Galerula*¹ is a genus of yellow-spored Agaricaceæ including small plants or those of medium size, but slender in form, and fragile. The species have no claim to rank of economic importance, while their ecological rôle as saprophytes is not large, owing to the comparatively small number of individuals. Many species are usually associated with mosses on logs or ground in the woods or swamps. A number of species occur on dung heaps or in recently manured grass lands. The larger number of species are some shade of yellow, or tawny, or ochraceous. In taxonomic works the genus is usually divided into sections according to external characters and ecological relations. By this method the species are not grouped according to their real affinities, and in a few cases forms not closely related are assembled under a single specific name.

A high degree of internal structural differentiation has taken place in the evolution of the species. In the present study this vantage point has been employed to group the species into sections more nearly in accord with their true relationships.

In some respects the genus, as usually recognized, occupies the same position in the yellow-spored Agarics that *Mycena* does in the white-spored group. The pileus is usually campanulate; the stem

¹ *Galera* Blume, *Bijdr.*, 415, 1825, is employed for a genus of orchids. *Galera*, by Fries in *Syst. Myc.*, 2: 264, 1821, as a tribe of *Agaricus*, was raised to generic rank by Quélet in 1872 ("Champ. Jura et Vosges," 135). Therefore while *Galera* Fries antedates *Galera* Blume by four years, it was used as a subgenus, or tribe, and cannot take precedence over *Galera* Blume, in accordance with rule 49 of the International Rules for Botanical Nomenclature. *Galerula* was employed by Karsten (*Bidr. Finl. Nat. Folk.*, 32, 442) in 1879 as a genus for several species which he separated from *Galera*. *Galerula* Karsten is employed here in the broader sense of the genus with practically the same limits as used by Murrill in 1917 ("N. Am. Fl.," 10, 161, 1917).

has a cartilaginous rind; in the young stage the margin of the pileus is straight, lying parallel with the stem, i. e., the margin not being incurved; a distinct veil is usually absent, or if present it is not usually of sufficient tenacity to form a distinct annulus on the stem. This feature of the straight pileus margin is often difficult to determine, since, in many cases, the number of individuals of a species collected is often too few, and they are in a too advanced stage of development to determine the relation of the pileus margin to the stem. Nevertheless, to one possessing some familiarity with the genus, the external form or "habit" of the plants, taken in conjunction with their color, serves in a large number of cases as a reasonably sure provisional means of differentiation from the related genera.

In some well-recognized species of the genus, however, the margin of the pileus is incurved in the young stages and never becomes straight. A notable example is *Galerula angusticeps*. Furthermore, there appear to be structural characters of great importance which indicate that certain species with a convex pileus, or a few with the margin incurved when young, are more closely related to the *Galerula* type than to other types, for example, certain species which, on the basis of the "habit" principle would fall in the genus *Naucoria*, *Pluteolus*, or even *Hebeloma*; while a few species placed in *Galerula* because of the "habit" formula, are excluded when the morphological, or structural, principle is employed as the basis of determining relationships.

On the basis of the morphological principle the species can be arranged in two groups. First, those in which the pileus is homogeneous, and second, those in which the pileus is corticated. This principle of grouping the species was, in fact, employed a quarter of a century ago by Fayod² who carried the principle still further by recognizing two generic concepts. He recognized *Conocybe* for the species with a corticated pileus, and *Galera* for those with a homogeneous pileus.

In his concept of the genus *Conocybe*, the cortex of the pileus was merely indicated as "pseudoparenchymatous." This definition

² Fayod V., "Prodrome d'une histoire naturelle des Agaricinés," *Ann. Sci. Nat. Bot.*, VII., 9: 181-411, 1889.

of the cortex does not appear to be sufficiently clear, and does not separate the true species of this section of *Galerula* from species of *Naucoria* and *Hebeloma* having a more or less pseudoparenchymatous cortex. According to the principle followed in the present arrangement, the cortex of the pileus in this section of the genus is more highly differentiated than the simple pseudoparenchymatous cortex. There is an outer layer clavate to pyriform cells, in the young stage forming a more or less definite palisade layer. In age these cells in certain species swell to a large size, as well as certain cells beneath this layer, so that the cortex takes on a pseudoparenchymatous aspect, but close examination shows the large pyriform cells of the surface, and it can be seen that the pseudoparenchyma is of a different origin and structure from that which I have termed simple pseudoparenchyma in certain species of *Naucoria* and *Hebeloma*.

Still further differentiation is manifest in the structure of the lamellæ. All species recognized here as belonging to *Galerula* are provided with specialized cells in the hymenium, usually termed *cystidia*. These vary in form and in their distribution on the lamellæ. They will not be discussed in detail at the present time. In the synopsis of the species presented below their form and arrangement is clearly indicated. The species with a corticated pileus are regarded as more highly specialized, those of the last section having reached the highest stage of specialization with corticated pileus and lecythiform or stopper-shaped cystidia. This specialization is further indicated by the large number of species with two-spored basidia.

There appear to be rather clear evidences of progression in development from the simpler forms of the species with a homogeneous pileus, and diverging in two lines, one line culminating in the corticated species, the other line retaining the homogeneous structure of the pileus. *Galerula angusticeps* proves to be an interesting species in this connection. Some individuals have the pileus homogeneous in structure, while others show a rudimentary cortex of the *Galerula* type. It is therefore placed in both of the principal groups in the synopsis. After a critical study of the species in allied genera has been made, it may be possible to make some suggestions concerning the relationships within the group.

This structural study of the genus *Galerula* in North America is based on an examination of material collected by myself during many years in this country and in Europe. The latter material was collected principally in Sweden and France. The determinations were confirmed or made by Dr. Robert Fries, son of Elias Fries for the species from Sweden, and by E. Boudier for the species from France. Through the courtesy of the State Botanist, Dr. H. D. House, I have had the opportunity of examining Dr. Peck's types in the State Museum at Albany. Through the courtesy of Dr. N. L. Britton, director of the New York Botanical Garden, and Dr. W. A. Murrill, I have examined also nearly all of the types in the Herbarium of the N. Y. Bot. Gard., and some European species.

There are 58 species from North America in the following synopsis.

SYNOPSIS OF THE SPECIES.

PILEUS HOMOGENEOUS.

Cystidia flask-shaped-lanceoloid-fusoid.

Cystidia on sides and edges of lamellæ.

I.

***Galerula besseyi* (Pk.) Murr. N. Am. Fl. 10, 163, 1917.**

Galera besseyi Peck, N. Y. State Mus. Bull. 131, 35, pl. 5, figs. 15-20, 1909.
Nebraska.

***Galerula hypnorum* (Fr. emend. Pat.) Atkinson.**

Agaricus (Galera) hypnorum Fr. ex Schrank. Syst. Myc. 1: 267, 1821.

Galera hypnorum Quélet Champ. Jura et Vosges, 1: 137, 1872;
Emend Patouillard, Tab. analyt. Fung. 1: 103, fig. 230, 1884.

Galerula hypni Murr. pr. pte. N. Am. Fl. 10: 163, 1917.

Galerula reflexa Murr. N. Am. Fl. 10: 169, 1917.

Oregon, Mexico, Europe.

***Galerula muricellospora* nov. sp.** Gregaria vel solitaria: 4-7 cm. alta: pileo campanulato, interdum convexo, hygrophano, striato,

fulvo vel ochraceo, demum pallidiore, glabro, homoganeo, 3–6 mm. lato, 3–5 mm. alto: lamellis stipite adnaxis vel anguste adnatis, subventricosis, subdistantibus, pallide ochraceis: cystidiis in superficie et in acie lamellarum, sublancoideis vel subfusoides, ad basem subventricosis, $40-90 \times 10-15 \mu$: sporis binis, ferrugineis, ovatis vel late subfusoides, a latere inequilateralibus, demum minute echinulatis, $10-14 \times 6-9 \mu$: stipite æquali, recto vel flexuoso, ochraceo-brunneo, sursum pallide luteo et pruinoso, fistuloso, 1–1.5 mm. crasso.

No. 7837, type, C. U. Herb., among living mosses, Coy Glen, near Ithaca, N. Y. Oct. 12, 1901. J. M. Van Hook collector.

New York, Colorado.

Galerula paludicola nov. sp. Gregaria vel dispergens, 5–13 cm. alta: pileo campanulato, dein convexo-expanso et umbonato, 1–2.5 cm. lato, hygrophano, ochraceo, striatulo, demum ochroleuco, homoganeo: lamellis stipite adnatis, leniter emarginatis, pallide-ochroleucis vel pallide-brunneis: cystidiis in superficie lamellarum subfusoides, $45-50 \times 10-12 \mu$: in acie lamellarum cystidiis similaribus: sporis quaternis, subellipsoideis, $10-14 \times 6-7 \mu$: stipite æquali, interdum bulbilloso, leniter floccoso-squamoso, luteo vel rubescente-luteo, deorsum obscuriore, 2–3 mm. crasso.

23576, type, C. U. Herb., among sphagnum, Malloryville Moor between McLean and Cortland, N. Y. Oct. 17, 1913. G. F. Atkinson collector.

New York.

Cystidia only on edges of lamellæ.

II.

Galerula cerina (Bres.) Atkinson nov. sp.

Galera cerina Bresadola n. sp. "in Herbario non publicaris."

Gregaria, 1.5–4 cm. alta: pileo campanulato vel convexo, obtuso, interdum subumbonato, glabro, striato, 2–8 mm. lato, 2–5 mm. alto, hygrophano, ochraceo-fulvo vel pallide ochraceo, demum ochroleuco, homoganeo: lamellis stipite adnatis, subventricosis, pileo concoloribus: cystidiis solum in acie lamellarum, numerosis, subcylindricis, ad basem subventricosis, interdum subcapitatis, rectis vel flexuosis, $30-60 \times 8-12 \mu$: sporis quaternis, ferrugineis vel ochraceo-fulvis, ovatis vel subnavicularibus, ad basem latioribus, levibus, $8-14 \times 6-8 \mu$: demum membrana sporæ rugulosa vel saccata: stipite æquali, subbulboso, pileo concolore vel decorum obscuriore, sursum pruinoso, 1 mm. crasso.

No. 25019, type, C. U. Herb., on humus near sphagnum in swamp 2.5 miles south of Oakland, Md. Sept. 16, 1917. G. F. Atkinson collector.

Maryland, North Carolina, New York.

Galerula coniferarum Murr. N. Am. Fl. 10, 162, 1917.

New York.

Galerula hemispherica Murr. N. Am. Fl. 10, 164, 1917.

New York.

Galerula heterocystis nov. sp.

Galerula hypni Murr. pr. pte. N. Am. Fl. 10, 163, 1917.

Forma et color *Galerulæ hypnorum*: cystidiis in acie lamellarum confertissimis, in superficie nullis, tibiiformibus vel clavato-mucronatis, $25-40 \times 10-14 \mu$: sporis quaternis, ovatis, a latere inequilateralibus, $12-15 \times 6-7 \mu$.

Type "Fungi of Jamaica, No. 435, Cinchona, 4,500-5,200 ft. alt.," N. Y. Bot. Gard. Herb.

Galerula inculta (Pk.) Murr. N. Am. Fl. 10, 165, 1917.

Galera inculta Peck, N. Y. State Mus. Ann. Rep. 41, 169, 1888.

New York.

Galerula lignicola Murr. N. Am. Fl. 10, 165, 1917.

New York.

Galerula minuta (Qué.) n. comb.

Galera minuta Quélet, Champ. Jura, Vosges, 3, 438, pl. 1, fig. 5, 1875.

New York.

Galerula parvula Murr. N. Am. Fl. 10, 162, 1917.

Tennessee.

Galerula sphagnicola nov. sp. Gregaria vel solitaria, 5-8 cm. alta: pileo campanulato dein expanso, umbonato, 1.5-2.5 cm. lato,

hygrophano, cinnamomeo-brunneo, striato, demum pallidiore: contexto homoganeo: lamellis stipite adnexis, in lineis decurrentibus, distantibus, cinnamomeo-brunneis, cystidiis solum in acie lamellarum, numerosis, crassis, cylindricis et deorsum ventricosis, interdum flexuosis, $30-45 \times 9-12 \mu$: sporis quaternis, ovalibus vel subnavicularibus, ad basem crassioribus, $8-11 \times 6-8 \mu$: membrana sporæ interdum rugulosa vel subinflata: stipite æquali, pileo concolore sed interdum pallidiore, demum pallide-cinnamomeo, glabro, sursum pruinoso, cavo, 2-4 mm. crasso.

No. 18587, type, C. U. Herb., among sphagnum in very wet places, Junius, N. Y. Sept. 15, 1904. H. H. Whetzel and H. S. Jackson collectors.

New York, Alabama.

Galerula sphagnorum (Fr. ex Pers.) Murr. N. Am.

Fl. 10: 167, 1917, emend Atkinson.

Agaricus hypnorum sphagnorum Pers. Syn. Fung. 386, 1801. Name only. Type not determined.

Agaricus hypnorum sphagnorum Fr. Syst. Myc. 1, 267, 1821. Name only.

Agaricus sphagnorum Lasch, Linnaea, 3: 417, 1828.

Galera sphagnorum Sacc. Syll. Fung. 5: 869, 1887.

Galera hypnorum var. *umbonata* Peck, N. Y. State Mus. Bull. 25, 655, 1899.

Maryland, New York, Europe.

Galerula subhypnorum nov. sp.

Galerula hypni Murr. pr. pte. N. Am. Fl. 10, 163, 1917.

Gregaria vel dispergens, 2-6 cm. alata: pileo campanulato-convexo, obtuso vel umbonato, ad marginem striato, hygrophano, fulvo vel ochraceo-fulvo, demum pallidore, homoganeo, 4-10 mm. lato: lamellis stipite adnatis, subdistantibus, ochraceo-fulvis: cystidiis solum in acie lamellarum, numerosis, lanceoloideis vel subcylindricis et ad basem subventricosis, in apice interdum crassioribus, $40-70 \times 6-11 \mu$: sporis quaternis, ochraceis, a fronte subellipsoideis vel subfusoides, a latere leniter inequilateralibus, levibus, $10-14 \times 6-8 \mu$: stipite pileo concolore sed pallidiore, ad basem interdum obscuriore, cavo, 1 mm. crasso.

This species differs from *G. hypnorum* in the absence of cystidia

on the sides of the gills, in their different form, and in the lighter-colored, thinner-walled spores.

New York, Maine, Washington, Europe.

Cystidia tibiiform, only on edges of lamellæ.

III.

Galerula bryophila (Pk.) nov. comb.

Galera bryophila Peck, N. Y. State Mus. Ann. Rept. 54, 149, 1901.

Galerula hypni Murr. pr. pte. N. Am. Fl. 10: 163, 1917.

New York, Colorado, Mexico.

Galerula lasiosperma nov. sp. Gregaria vel solitaria, 6–9 cm. alta: pileo ovali-campanulato, dein convexo et expanso, obtuso, hygrophano et ad marginem striatulo, 1 cm. lato, 4–5 mm. alto, castaneo, demum fulvo vel ochraceo-fulvo, homoganeo: lamellis stipite adnatis, ventricosis, subdistantibus, ochraceis: cystidiis solum in acie lamellarum, tibiiformibus, ad basem subventricosis, sersum teretibus et capitatis, $30-45 \times 6-8 \mu$: sporis quaternis, ferrugineis, ovalibus vel subreniformibus vel fabiformibus, leniter echinulatis, $7-11 \times 5-7 \mu$: stipite æquali, recto vel flexuoso, pileo concolore sed pallidiore, sursum pruinoso, ad basem albo-myceleoideo, cavo, 1–1.5 mm. crasso.

No. 25033, type, C. U. Herb., on sphagnum in open field, Teet's Farm, Cranesville moor, Western Maryland. Sept. 18, 1917. G. F. Atkinson collector.

Maryland.

Galerula lenticeps (Pk.) nov. comb.

Agaricus lenticeps Peck, N. Y. State Mus. Ann. Rept. 31, 34, 1879.

Naucoria lenticeps Sacc. Syll. Fung. 5, 838, 1887.

New York.

Galerula pistillicystis nov. sp. Gregaria, 2–3 cm. alta: pileo hemisphaerico-campanulato, 4–10 mm. lato, hygrophano, striato, luteo, dein pallide ochraceo, homoganeo: lamellis stipite adnatis, subventricosis, ferrugineis: cystidiis solum in acie lamellarum, numerosis, pistilliformibus, ad basem ventricosis, sursum teretibus et capitatis, $25-35 \times 6-8 \mu$: sporis quaternis, ferrugineis, subellipsoideis, levibus, $7-10 \times 3.5-5 \mu$: stipite æquali, pileo concolore sed pallidiore, glabro, sursum pruinoso, cavo, 1 mm. crasso.

No. 24072, type, C. U. Herb., on a rotten log among mosses, in a

swamp bordering on Labrador Lake, near Apulia, Onondago Co., N. Y. June 12, 1917. G. F. Atkinson collector.
New York.

Galerula rufipes (Pk.) Murr. N. Am. Fl. 10, 164, 1917.

Galera rufipes Peck, N. Y. State Mus. Ann. Rept. 42, 116 (20), 1889.
New York.

Galerula semilanceata (Pk.) n. comb.

Galera semilanceata Peck, Torr. Bot. Club Bull. 23, 415, 1896.
Washington.

Galerula styliifera nov. sp. Gregaria, 3–5 cm. alta: pileo ovali dein campanulato, matura expanso et subumbonato, 1–2 cm. lato, hygrophano, ochroleuco-fulvo vel pallide-ochraceo, demum ochroleuco, glabro, homoganeo: lamellis stipite adnatis, emarginatis, ventricosus, ochraceis: cystidiis solum in acie lamellarum numerosis, styliiformibus vel tibiiformibus, ad basem subventricosus, apice capitato, $30-45 \times 5-8 \mu$: sporis quaternis, ochraceis, subellipsoideis, $6-8 \times 3.5-4.5 \mu$: stipite æquali, ochraceo-fulvo vel castaneo, subvillosus, sursum pruinoso, 2 mm. crasso.

No. 24399, type, C. U. Herb., on very rotten wood mold and decaying leaves of *Pinus strobus*, McGowan's Woods, near Ithaca, N. Y. Oct. 10, 1917. H. E. Stork collector.
New York.

Galerula subannulata nov. nom.

Naucoria lateritia Murr. N. Am. Fl. 10, 172, 1917.
Maryland, New York.

Galerula tibiicystis nov. sp. Gregaria, 6–9 cm. alta: pileo campanulato dein convexo et interdum umbonato, 1–2 cm. lato, hygrophano, fulvo, glabro, demum pallido-ochraceo, homoganeo: lamellis stipite adnatis uncinatis, ventricosus, subdistantibus: cystidiis solum in acie lamellarum, numerosis, tibiiformibus, ad basem subventricosus, apice capitato, $30-45 \times 7-9 \mu$: sporis quaternis, ovatis vel subellipsoideis, a latere inequilateralibus, ferrugineis, $8-12.5 \times 5-7.5 \mu$: stipite æquali, pileo concolore sed pallidiore, sursum pruinoso, 2–2.5 mm. crasso.

No. 25080, type, C. U. Herb., on sphagnum in a spruce moor

near Miller's Run, 3-4 miles north of Oakland, Md. Sept. 25, 1917.
G. F. Atkinson collector.

Maryland, New York, Massachusetts, Sweden (Upsala).

Cystidia lecythiform or stopper-shaped, only on edge of lamellæ.

IV.

Galerula angusticeps (Pk.) Murr. N. Am. Fl. 10, 168, 1917.

Galera angusticeps Peck, Torr. Bot. Club Bull. 24, 143, 1897.

Conocybe angusticeps Murr. Mycologia, 4, 248, 1912.

California.

Galerula teneroides (Pk.) Murr. N. Am. Fl. 10, 166, 1917.

Agaricus teneroides Peck, N. Y. State Mus. Rept. 29, 39, 1878.

Galera teneroides Sacc. Syll. Fung. 5, 861, 1887.

This species is placed here provisionally. The portion of the type material examined was in such poor condition that the structure of the pileus could not be determined.

New York.

PILEUS CORTICATED.

Cystidia large, fusoid or clavate, or sublanceoloid, not specialized.

Cystidia on sides and edges of lamellæ, emerging.

V.

Galerula kellermani (Peck) Murr. N. Am. Fl. 10, 165, 1917.

Galera kellermani Peck, Jour. Myc. 12, 148, pl. 89, 1906.

Ohio.

Galerula cervinialba (Murr.) nov. comb.

Prunulus cervinialbus Murr. N. Am. Fl. 9: 326, 1916.

Cystidia subfusoid: basidia large, sterile, therefore the pure white lamellæ.

New York.

Cystidia only on edge.

VI.

Galerula cyanopus nov. sp. Gregaria vel solitaria, 2–3 cm. alta: pileo ovali, campanulato-convexo, dein expanso, obtuso, ad marginem striatulado, fragili, brunneo-ferrugineo, 5–10 mm. lato: cortice pilei cellis pyriformibus prædito: lamellis stipite adnexis, angustatis, ochraceis: cystidiis in acie lamellarum numerosis, ad basem ventricosis, in apice cylindricis vel mucronatis, $30-40 \times 10-17 \mu$: sporis quaternis, ellipsoideis, apice minute truncato, $8-10 \times 5-6 \mu$: stipite 1–1.5 mm. crasso, leniter bulboso, albo ad basem cyaneo, sursum pruinoso, deorsum leniter velutino, fragili.

Ground among grass, No. 23302, type, C. U. Herb., Ithaca, N. Y. New York.

Galerula filipes nov. sp. Gregaria, 4–6 cm. alta: pileo ovali dein campanulato, obtuso, ochraceo, 3–6 mm. lato: cortice pilei cellis obovalibus vel pyriformibus prædito: lamellis stipite late adnatis, dente decurrentibus, ochraceis vel ochraceo-fulvis: cystidiis solum in acie lamellarum, lanceoloideis vel anguste ovatis, ad basem ventricosis, $30-50 \times 10-18 \mu$: sporis quaternis, ferrugineis vel fulvo-ochraceis, ellipsoideis, $7-8 \times 4-5 \mu$: apice sporæ truncato: stipite æquali, bulbilloso, sursum pruinoso, 1 mm. crasso.

The type material consists of specimens collected by Peck in a grass plot at North Elba, Essex Co., Adirondack Mts., N. Y., now in the N. Y. State Mus., Albany, as *Galera capillaripes* (see N. Y. State Mus. Bull. 94: 32, 1905).

This species resembles in form and color *Galerula capillaripes*, but the basidia are four-spored, the spores are much smaller and the cystidia are different.

New York.

Galerula mirabilis nov. sp. Gregaria vel dispergens, 4–6 cm. alta: pileo campanulato-convexo, dein expanso et umbonato, 1.5–2 cm. lato, glabro, striatulo vel rugoso, vinaceo-cinnamomeo, in centrum castaneo, cortice cellis obovalibus vel pyriformibus prædito: lamellis stipite adnexis, subdistantibus, subventricosis, fulvo-ochraceis, acie lamellarum alba: cystidiis solum in acie lamellarum, numerosis, abrupte clavatis, $40-70 \times 12-18 \mu$: sporis binis, a fronte navicularibus vel cymbiformibus, a latere inequilateralibus, demum minute tuberculatis, fulvis, $12-25 \times 7-11 \mu$: stipite æquali, recto vel flexuoso, cavo, glabro, pileo concolore sed pallidiore, sursum pruinoso.

No. 15117, type, C. U. Herb., in mixed woods in a swamp near McLean, N. Y. June 17, 1903. H. H. Whetzel collector.

New York.

Galerula plicatella (Pk.) Murr. N. Am. Fl. 10: 164, 1917.

Agaricus coprinoides Peck, Buffalo Soc. Nat. Sci. Bull. 1, 52, 1873.

Agaricus plicatellus Peck, N. Y. State Mus. Rept. 29, 66, 1878.

Galera coprinoides Sacc. Syll. Fung. 5, 867, 1887.

Galera plicatella Earle, Torreya 3, 136, 1903.

New York.

Galerula sulcatipes (Pk.) Murr. N. Am. Fl. 10, 166, 1917.

Agaricus sulcatipes Peck, N. Y. State Mus. Ann. Rept. 35, 132, 1884.

Galera sulcatipes Sacc. Syll. Fung. 5, 866, 1887.

New York.

This species is very closely related to *Galerula tortipes*, from which it differs only in its smaller size.

Galerula tortipes (Mont.) Murr. N. Am. Fl. 10, 167, 1917.

Agaricus tortipes Mont. Syll. Crypt. 119, 1856.

Galera tortipes Sacc. Syll. Fung. 5, 867, 1887.

Ohio.

Galerula viscosa (Clem.) nov. comb.

Galera viscosa, Clements, Cryp. Form. Coloradensum, No. 380, 1906.

Colorado.

**Cystidia specialized, lecythiform or stopper-shaped,
on edge of lamellæ.**

*Cystidia on sides imbedded, clavate or clavate mucronate,
on edge lecythiform or stopper-shaped.*

VII.

Galerula cryptocystis nov. sp. Gregaria, 6–10 cm. alta: pileo ovali dein campanulato, 1.5–2.5 cm. lato, ochraceo, ochraceo-fulvo vel ferrugineo, demum pallidiore, sparsim villosa: cortice pilei cellis pyriformibus vel ovalibus prædito: lamellis stipite adnexis, latis: cystidiis in acie lamellarum lecythiformibus, $15-22 \times 6-8 \mu$, in superficie lamellarum clavatis, non projicientibus: sporis binis, a fronte late ellipsoideis, $12-22 \times 8-12 \mu$: stipite æquali, pileo concolore sed pallidiore, striato, sursum pruinoso, 2–4 mm. crasso.

No. 127, Pacific Slope Fungi, distributed as "*Galera tenera*" by C. F. Baker, type in C. U. Herb. "A common little mushroom on decayed horse manure in old pastures. Foothills near Stanford University, Santa Clara County, California, November 30, 1901, Coll. C. F. B."

This species is related to *Galerula macrospora*, but differs in the striate stem, imbedded cystidia on the sides of the lamellæ, etc.

California, Europe (Trento, May, 1901, Bresadola).

Cystidia only on edge.

VIII.

***Galerula angusticeps* (Pk.) nov. comb.**

See above under section IV. Pileus homogeneous. Some specimens have a rudimentary cortex.

***Galerula antipus* (Lasch) emend Atkinson.**

Agaricus antipus Lasch in Linnaea, 3, 415 (no. 401), 1828.

Galera antipus Quél. Champ. Jura et Vosges, 1, 136, 1872.

Galera antipus Gillet, Champ. France, 553, with figure, 1878.

Galera antipoda Sacc. Syll. Fung. 5, 863, 1887.

Spores in front view limoniform to subangular, in side view ellipsoid.

North Carolina.

***Galerula capillaripes* (Pk.) Murr. N. Am. Fl. 10, 163, 1917.**

Galera capillaripes Peck, Torr. Bot. Club Bull. 26, 166, 1899.

Ohio, New York.

***Galerula crispa* (Longyear) Murr. pt. pte.**

N. Am. Fl. 10, 167, 1917.

Galera crispa Longyear, Bot. Gaz. 28, 272, 1899.

Michigan, New York.

Galerula crocospora (Berk. & Curt.) Murr.

N. Am. Fl. 10, 168, 1917.

Agaricus crocosporus B. & C. Ann. Mag. Nat. Hist. II, 12, 421, 1853.*Galera crocospora* Sacc. Syll. Fung. 5, 866, 1887.

South Carolina. This species probably belongs here but the type material examined was too badly collapsed to determine with certainty.

Galerula curta nov. sp. Gregaria, 4–6 cm. alta: pileo campanulato dein subexpanso, 2–4 cm. lato, 1–2 cm. alto, obtuso, glabro, non striato, ochraceo vel ochraceo-fulvo demum ochroleuco, cortice pilei cellis obovalibus vel pyriformibus prædito: lamellis stipite adnexis, ellipsoideis, ochraceis: cystidiis solum in acie lamellarum, numerosis, lecythiformibus, $15\text{--}25 \times 7\text{--}10 \mu$: sporis binis, obovalibus vel late ellipsoideis, ochraceis, $10\text{--}18 \times 8\text{--}11 \mu$: stipite æquali, glabro, striatulo, sursum pruinoso, cavo, 3–5 mm. crasso.

Nos. 3209 and 3210, type, C. U. Herb., in grass in curbing at foot of Buffalo St., Ithaca, N. Y. July 20, 1899. G. F. Atkinson collector.

New York.

Galerula distantifolia Murr. N. Am. Fl. 10, 169, 1917.

Mexico.

Galerula flava (Pk.) Murr. N. Am. Fl. 10, 166, 1917.*Galera flava* Peck, N. Y. State Mus. Ann. Rept. 45, 79, (19) 1893.

New York.

Galerula flexipes (Karst.) nov. comb.*Galera flexipes* Karsten, Myc. Fenn. 3, 371.

New York.

Galerula fragilis (Pk.) Murr. N. Am. Fl. 10, 164, 1917.*Galera fragilis* Peck, Torr. Bot. Club Bull. 24, 144, 1897.

Kansas.

Galerula "lateritia." A medium-sized *Galerula* very closely related to *Galerula crispa*, which may be only a variety. It is usually regarded in this country as equal to *Agaricus lateritius* Fr.; I am not

at present convinced of the correctness of this interpretation. It is common in lawns and grassy places in rainy weather, May to July, and also occurs on dung.

***Galerula macrospora* nov. sp.**

Galera tenera obscurior Peck, N. Y. State Mus. Rept. 50, 130, 1899.

Gregaria, 6–15 cm. alta: pileo campanulato, 1–2.5 cm. lato, 6–10 mm. alto, ochraceo vel ferrugineo, non striato, demum ochroleuco, cortice pilei cellis pyriformibus vel obovatis prædito: lamellis stipite adnexus, ellipsoideis, ochraceis: cystidiis solum in acie lamellarum, numerosis, lecythiformibus, $15-25 \times 6-9 \mu$: sporis binis, late ellipsoideis, $12-25 \times 8-15 \mu$: stipite æquali, recto vel flexuoso, sursum pruinoso, pileo concolore, cavo, 1.5–2.5 mm. crasso.

No. 15759, type, C. U. Herb., on ground among mixed grasses and moss (*Hylocomium squarrosus*), on the edge of a coniferous wood, near Stockholm, Sweden. Aug. 24–28, 1903. G. F. Atkinson collector.

North America (New York), Europe (Sweden and France).

***Galerula mexicana* Murr. N. Am. Fl. 10, 169, 1917.**

Mexico.

Galerula neoantipus nov. sp. Gregaria, 3–7 cm. alta: radix 2–5 cm.: pileo campanulato-convexo, 1.5–2.5 cm. lato: cortice pilei pseudoparenchymato: lamellis cum in *Galerula antipus*: cystidiis solum in acie lamellarum, numerosis, lecythiformibus, $15-30 \times 6-9 \mu$: sporis quaternis, ellipsoideis, $12-17 \times 6-9 \mu$.

On newly seeded lawn, Middlebury, Vt., Aug. 1896, E. A. Burt collector, in E. & E. N. Am. Fungi, second edition, No. 3510, type, C. U. Herb. The specimens in Cooke's Ill. Brit. Fungi, No. 463, "spores ellipsoid, $16 \times 8 \mu$," probably belong here.

Vermont, (?England).

***Galerula ovalis* (Fr.) Karsten, Bidr. Finl. Folk 32, 443, 1879.**

Agaricus (*Galera*) *ovalis* Fr. Monogr. Hymen. Suec. 1, 389, 1857.

Galera ovalis (Fr.) Gillet, Champ. France 3, 554, 1876.

New York, North Carolina, Europe.

Galerula pilosella (Fr. ex Pers.) Atkinson emend.

Agaricus (*Galera*) *tener* var. *pilosellus* Fr. Syst. Myc. 1, 266, 1821.

Agaricus pilosellus Pers. Synop. Fung. 387, 1808.

Gregaria vel *solitaria*, 3–6 cm. alta: pileo campanulato, ad marginem interdum expanso, 1–2.5 cm. lato, 1 cm. alto, hygrophano, ochraceo vel cinnamomeo-brunneo, striatulato, demum pallide ochraceo vel fulvo-ochraceo, leniter villosus: cortice pilei cellis pyriformibus et rare cystidiis prædito: lamellis stipite adnexus, angustatis, ellipsoideis, numerosis, luteo-ochraceis vel ochraceo-cinnamomeis: cystidiis in acie lamellarum lecythioideis, $15-24 \times 6-9 \mu$: sporis quaternis, anguste ellipsoideis, apice minute truncato, $6-8 \times 3-4 \mu$: stipite æquali, subtiliter villosus.

No. 20851, C. U. Herb., type of the emended species, on ground in a spruce forest north of Pontarlier, Jura Mts., France, Aug. 21, 1905, G. F. Atkinson collector. No. 24314, C. U. Herb., near Seventh Lake, Adirondack Mts., N. Y. Aug. 15, 1917. G. F. A. and F. C. Stewart collectors.

New York, Maryland, Europe.

Galerula plumbeitincta nov. sp. *Gregaria*, 3–5 cm. alta: pileo convexo, dein campanulato, 1–1.5 cm. lato, adolescente lubrico, substriato, plumbeitincto, cortice cellis clavato-pyriformibus prædito: lamellis stipite late adnatis, subdistantibus, ventricosis, ochraceo-cinnamomeis: cystidiis solum in acie lamellarum, numerosis, ampullæformibus, frequenter subcapitatis, $25-35 \times 12-15 \mu$: sporis quaternis, ochraceo-cinnamomeis, late ellipsoideis, $12-15 \times 7-10 \mu$: stipite albo dein plumbeitincto, sursum pruinoso, deorsum substriato, cavo, 2–3 mm. crasso.

On dung hills, Cascade Glen, Ann Arbor, Mich. June 9, 1906. C. H. Kauffmann collector, no. 565, type, C. U. Herb.

Michigan.

Galerula procera nov. sp. *Gregaria*, 10–12 cm. alta: pileo campanulato, obtuso, ad marginem demum leniter expanso, 3–4.5 cm. lato, 2–2.5 cm. alto, ochraceo-fulvo, dein ochraceo vel pallide ochroleuco, glabro, non striato: cortice pilei cellis obovalibus vel pyriformibus prædito: lamellis stipite adnexus, ellipsoideis, ochraceis: cystidiis solum in acie lamellarum, numerosis, lecythiformibus, $18-25 \times 6 \mu$: sporis quaternis, ochraceis, a fronte late ellipsoideis, apice minute truncata, $12-20 \times 8-11 \mu$: stipite æquali, ad basem leniter crasso, recto vel flexuoso, glabro, striato, sursum pruinoso, pileo concolore sed pallidiore, 3–4 mm. crasso.

No. 9910, type, C. U. Herb., on ground, in humus, among leaves in moist woods, Buttermilk Gorge, near Ithaca, N. Y. July 23, 1902. C. H. Kauffmann collector.
New York.

Galerula pulchra (Clem.) Murr. N. Am. Fl. 10, 166, 1917.

Galera pulchra Clements, Bot. Surv. Nebr. 4: 22, 1896.
Nebraska.

Galerula spartea (Fr.) nov. comb.

Agaricus (*Galera*) *sparteus* Fr. Syst. Myc. 1: 266, 1821.
Galera spartea Quélet, Champ. Jura, Vosg. 1: 254, 1872.
New York.

Galerula tenera (Fr. ex Schaeff.) Murr.
N. Am. Fl. 10, 166, 1917.

Agaricus (*Galera*) *tener* Fr. Syst. Myc. 1, 265, 1821.
Galera tenera Quélet, Champ. Jura et Vosges, 136, 1872.
Throughout greater part of N. Am., Europe.

Galerula tenerella (Atkinson) Murr. N. Am. Fl. 10, 164, 1917.

Galera tenerella Atkinson, Ann. Myc. 7, 369, 1909.
New York.

Galerula tenuissima (Weinm.) nov. comb.

Agaricus tenuissimus Weinm. Fl. Ross, 219, 1836.
Galera tenuissima Quélet, Assoc. Fr. Av. Sci. 1884, 280, pl. 12, fig. 8, 1885.
New York.

SPECIES NEEDING FURTHER STUDY.

GALERULA GLABRA Murr. N. Am. Fl. 10: 163, 1917, has not been examined.

GALERA GRISEA Earle, No. 43 Inform. An. Estac. Centr. Agron. Cuba 1: 237, 1906, needs further examination of fresh material.

PROC. AMER. PHIL. SOC., VOL. LVII, 2, AUG. 19, 1918.

GALERA SIMULANS Earle, Inform. An. Estac. Centr. Agron. Cuba
1: 236, 1906, is probably identical with *Galerula "lateritia."*

SPECIES EXCLUDED.

GALERA ALBA Peck, Torr. Bot. Club Bull. 24: 143, 1897.

AGARICUS (GALERA) CALLISTUS Peck, Buff. Soc. Nat. Sci. Bull.
1: 52, 1873.

AGARICUS (GALERA) EXPANSUS Peck, Buff. Soc. Nat. Sci. Bull.
1: 52, 1873.

GALERA RETICULATA Peck, N. Y. State Mus. Ann. Rept. 54: 150,
1901.

GALERA STRIATULA Clements, Bot. Surv. Nebr. 3: 13, 1894.

GALERA VERSICOLOR Peck, Torr. Bot. Club Bull. 24, 143, 1897.

CORNELL UNIVERSITY,
ITHACA, N. Y.,
May, 1918.

ORGANIZATION, REPRODUCTION AND INHERITANCE IN PEDIASTRUM.

(PLATES V. AND VI.)

By R. A. HARPER.

(Read April 19, 1918.)

I have discussed in previous papers ('08, '12) the problems of organization as seen in strictly cœnobic plants in which the colony shows little or practically no differentiation in either the structure or the functions of its cells. In *Pediastrum* we have a type in which at least the incipient steps in differentiation can be recognized.

The margins of the flat plate-shaped cell colonies are in some species quite entire, in others more or less lobed or toothed, and present the problems of the development and inheritance of specific and differentiated form in plants at a relatively critical stage. We have here the first beginnings of cell, and, we may say, tissue differentiation. In such cœnobes as most species of *Spirogyra*, *Hydrodictyon*, *Gonium* and others, though the colonies have definite and probably adaptive structure, the cells are all alike in form and function, but in certain species of *Pediastrum* the lobed peripheral cells differ markedly from the interior cells of the colony. In other species the lobing is almost equally developed in all the cells. The genus thus presents us with the processes of differentiation in varying degrees of expression in what are plainly rather closely related species.

I have also discussed elsewhere ('16) the interrelations of the cells in the eight- and sixteen-celled colonies of *Pediastrum Boryanum* as giving the basis for a definite conception of plant types and the comparison of this species with the other members of the group brings out still more clearly the idea of biological form types as I have discussed it there. The group is also well adapted to illustrate the relations of heredity and environment in morphogenetic

processes and to give evidence as to the possible mode of origin and interrelations of different types.

The shape of the cell is the main basis of group distinctions in the genus. As Braun ('55) first pointed out, the number of cells in the colony has been shown not to be diagnostic of species or larger aggregates. Fig. 21 shows two daughter colonies, one with sixteen and one with thirty-two cells, both of which came from the same thirty-two-celled mother colony. The shape of the cells of a given species varies in minor details of proportion about a norm for the species. The form of the cells of different species are of more fundamentally diverging types.

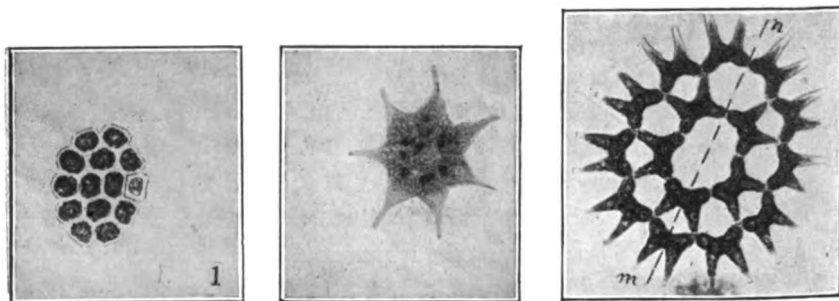


FIG. 1.

FIG. 2.

FIG. 3.

FIG. 1. *Pediatrulum integrum*. Cells almost without spines or lobes. The colony shows only fourteen cells but it is possible, as is common for this species, that it is partially two layered. \times about 225.

FIG. 2. *P. simplex*. Cells with one spine. Configuration 1 + 7. \times about 150.

FIG. 3. *P. clathratum*. Cells with two very long and slender peripheral and two shorter basal lobes, large intercellular spaces. Configuration 5 + 11. Colonies bilaterally symmetrical about the axis *m*, *n*. \times about 350.

It is a question of first importance morphogenetically whether these cell forms are hereditary or whether they are newly achieved under the stimulus of the intercellular environment in each generation. It is plain that the form is not inherited directly as such since the two-spined cells do not divide in such a way as to produce at once two equivalent two-spined daughter cells.

The main distinctions in the group are between forms whose cells have no spinous processes or very rudimentary ones, and those whose cells have more or less developed spines. These distinctions

have been regarded as of subgeneric rank and are the basis of the *integrum* (Fig. 1), Monactinia or *simplex* (Fig. 2), the Diactinia or two-spined (Fig. 3), the Triactinia or three-spined and the Tetractinia or four-spined series. A tendency to the formation of a four-spined type of cell is shown in the species *P. biradiatum* Meyen, and the peripheral cells of *P. tricornutum* Borge are described as having three spines. Braun ('55) recognized the diagnostic value of cell form in making four sections of the genus, the Monactinia, *P. Simplex*, Anomopodium, *P. integrum* (Näg.), the Diactinia, *P. Boryanum*, etc., and the Tetractinia, *P. Ehrenbergii*.

A further class of differences which has been given specific rank is found in the degree of similarity in form between all the cells of the colony. In *P. Boryanum* (Fig. 4) the interior cells are quite different in form from the peripheral series, while in *P. integrum* (Fig. 1), on the one hand, and *P. clathratum* (Fig. 3) on the other, the cells are very much alike throughout the colony.

It seems natural to assume that such forms as *P. integrum* (Fig. 1) with its oval cells, sometimes with two papillæ, but with no striking form differentiations, represent the more primitive species, though perhaps *P. integrum* itself is only an environmental form as I am suggesting in another paper, and that evolution has progressed toward the *simplex* type with one spine on the one hand, and the two-spined type on the other. The tendency to the development of spines more strongly on the peripheral cells probably came first (*P. Boryanum*, Fig. 4) and later the development of the strongly four-lobed form in all the cells of the colony (*P. clathratum*, Fig. 3). Positive evidence that the evolution of the group has followed this course is, however, lacking. The origin of the tendency to produce spines is also not obvious. We shall find a direct relation between the cell form and the intercellular relations in the colony in comparing the colonies of *P. Boryanum* (Fig. 4) and *P. asperum* (Fig. 5) and we have evidence for the assumption that the result of a direct environmental influence has been transformed into an inherited cell character in such cases but no support for such an hypothesis is found in the three-spined cells of *P. tricornutum* Borge or the four-spined cells of *P. biradiatum* Meyen.

As noted, the number of cells in a colony has been shown to

have relatively slight diagnostic value for the species. *P. asperum* like *P. Boryanum* may have eight, sixteen, thirty-two or sixty-four cells. Still certain species tend toward higher and others toward lower cell numbers. *P. Ehrenbergii* commonly occurs with four, eight, or sixteen cells. The rule that the number of cells in any species is a multiple of two, based as it is on the law of cellular bipartition, is very universally maintained and has long been recognized. Individuals with fifteen cells instead of sixteen cells or

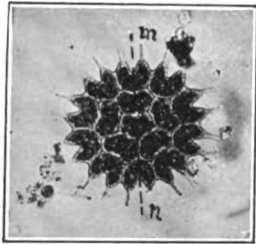


FIG. 4.

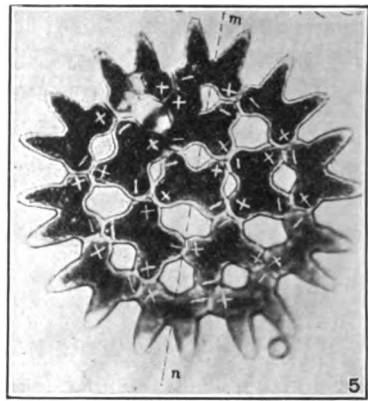


FIG. 5.

FIG. 4. *Pediastrum Boryanum*. Peripheral cells with two spines very slender for the species. Interior cells with merely a reëntering angle to indicate the spines. No intercellular spaces. Configuration $1 + 5 + 10$. Colony bilaterally symmetrical about the axis *m, n*. \times about 300.

FIG. 5. *P. asperum*. Cells with two fairly long peripheral spines and two short, blunt basal lobes. Intercellular spaces well developed, the curves which bound them suggesting the origin of the cell lobes by catenoidal deformation. Configuration $1 + 5 + 10$. Colony bilaterally symmetrical about the axis *m, n*. Possible polarities of the cells suggested by the plus and minus signs. \times about 600.

thirty-one instead of thirty-two cells occur, but as Nitardy ('14) has emphasized, they are great rarities and may be properly regarded as abnormal. The figure of *P. integrum* given shows only fourteen cells (Fig. 1).

The relative development of the spine is directly correlated with that of the intercellular spaces and we may consider first the organization of a form with well-developed intercellular spaces. Perhaps

the most abundant species as I have found them, next to *P. Boryanum* Kg., is *P. asperum* (Figs. 5 and 6). *P. asperum* has been regarded by many as a form of *P. Boryanum*. Whether or not it is to be considered a good species, the forms as I have found them reproduce the type so far as cell form, involving as it does the characteristic intercellular spaces, is concerned with a high degree of constancy. I have never seen a colony with the *asperum* cell form produced from a *Boryanum* parent nor a colony without intercellular spaces from an *asperum* parent.

I have been able to study and photograph *P. asperum* in all stages of the vegetative growth and reproduction of the colonies and it may well serve to illustrate the two-spined forms with well-developed intercellular spaces and cells similar throughout the colony in contrast with *P. Boryanum* with intercellular spaces small or wanting and interior cells only slightly or even not at all two-spined, as I have already described it ('16).

ARRANGEMENT OF THE CELLS AND INTERCELLULAR SPACES IN THE SIXTEEN-CELLED COLONIES OF *P. ASPERUM*.

The spatial interrelations of the cells are essentially the same in the typical sixteen-celled colony of *P. asperum* as in the typical sixteen-celled colony of *P. Boryanum*, as I have described it elsewhere ('16), and as it has long been known in the literature. But in *P. asperum* the cells are all very much alike in form, the interior cells having only slightly shorter lobes than those on the periphery of the colony. We may consider first the sixteen-celled colony, which is perhaps the most common, though 8-, 32-, 64- and 128-celled colonies are found. I shall leave the colonies with 32, 64, 128, etc., cells without discussion at this time, since certain further elements in morphogenesis implied in the larger number of units are involved which I shall take up in a later paper. A common arrangement in the thirty-two-celled colony is $1 + 6 + 10 + 15$, as noted by Braun ('55). The presence of six cells in series II. of the thirty-two-celled colony as compared with the five in series II. of the sixteen-celled colony introduces quite fundamentally different relations between the oblong four-lobed form of the cells and the natural surface tension factors in such groups.

As in *P. Boryanum*, the general arrangement of the cells in the most common form of sixteen-celled colony of *P. asperum* is one in the center with five around this and two cells in the third or outer series, the $1 + 5 + 10$ group, as Nägeli and Braun called it. Nägeli ('49, p. 93) quite fully described these conditions for the group and by comparing the areas of the concentric circles, assuming the radial diameters of the cells are the same, showed geometrically that these cell numbers are what he calls the "most natural," that is, the cells so arranged come the nearest to filling the spaces in the concentric circles as well as being the ones most commonly found. I have described this arrangement ('16) as coming the nearest to that of a least-surface configuration for such a group of rounded cells lying in one plane. As I shall further discuss in another connection, Nägeli is, however, probably mistaken, at least for *P. Boryanum*, as Braun's figures ('55) show, in saying that for eight cells the arrangement $2 + 6$ is much less common than the "more natural" arrangement $1 + 7$.

I shall follow the same method of numbering the cells here as in the case of *P. Boryanum* (Fig. 25, and '16, Fig. 1b), making the central cell No. 1 and proceeding outward as shown in the diagram (Fig. 7). The colony is bilaterally symmetrical as in *P. Boryanum*, the axis bisecting cells 1, 4, 7 and 12 and passing through the surface of contact of cells 2 and 6. For describing the structure of the colony more conveniently we may here, as in the case of *P. Boryanum*, call the ends of this axis of the colony its *m* and *n* poles respectively.

The central cell is in contact with five cells. The cells of the second series are each in contact with six cells and the cells of the outer series are alternately in contact with three and four cells. The cell walls meet in threes on the principle of least surfaces, except where cells 2 and 6 are in contact as a pair right and left of the axis of the colony. In *P. Boryanum* this grouping of intersections is universal in the more regular sixteen-celled colonies and the paired contact of cells 2 and 6 is one of the most obvious differences between the two species in their intercellular relations.

If the tips of the lobes of a cell of series II. be connected in serial order, g^1, g^2, d^3, d^2 , by straight lines, we have a trapezoid with

its longest side away from the center of the colony. In the case of the central cell we have a trapezoid with its longest side connecting the apices of the basal lobes. As in *P. Boryanum*, five of the outer cells stand radially outward from the five cells of series II. and five stand radially opposite the surfaces of contact of the cells of series II.

Cells eight and sixteen, nine and fifteen, ten and fourteen, eleven and thirteen are paired to the right and left of the axis of the col-

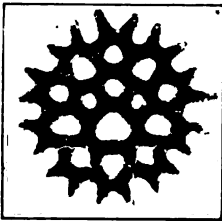


FIG. 6.

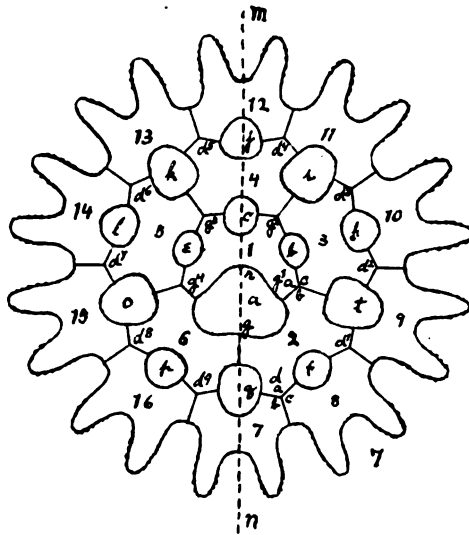


FIG. 7.

FIG. 6. *Pediastrum asperum*. Very typical colony organization as described for Fig. 5. This colony served as the model for the type diagram for the species given in Fig. 7. \times about 325.

FIG. 7. Type diagram for *P. asperum*. Angles of intersection of all the walls made 120° . Intercellular spaces and peripheral spines sketched free-hand from the colony shown in Fig. 6. Numbering of cells and lettering of angles as in diagram of *P. Boryanum*, fig. 35.

ony. The adaptive and symmetrical adjustment by which, with the products of cellular bipartition to be grouped, we get five instead of six cells in series II., thus leaving ten for series III., which can be so spaced as to place one cell opposite each cell of series II. and one cell opposite the surface of contact of each pair of cells in series

II., is just as conspicuous here as in the case of *P. Boryanum*. The delicacy of the pressure and contact responses which prevents the placing of six, the normal least-surface number, around the central cell, thus leaving only nine for the peripheral series, and resulting in quite asymmetric contact relations between series II. and III., affords good evidence of the efficiency of cellular interactions in the production of morphogenetic adjustments.

The four-lobed form of the cells and the spacing of the five cells of series II. about the central cell and the ten cells of series III. about the five cells of series II., leave free intercellular areas and the symmetrical distribution of these areas in such fashion as to maintain most perfectly the rigidity of the colony and the equality of the cells has led to the development of one of the very obvious differences between *P. asperum* and *P. Boryanum*. This is perhaps the most conspicuous difference between the two species. The cells instead of being in contact on the entire extent of their adjacent surfaces show a series of intercellular openings which perforate the plate-shaped colony like the holes in a sieve. An intercellular space is formed between each pair of contact walls of the sixteen cells. They are of such form and are so placed that the interior cells of the colony have the four-lobed form of the peripheral cells. The cells of the whole colony are thus, as noted above, much less differentiated in form than those of the colony of *P. Boryanum*. The inner cells differ from the outer cells, broadly speaking, only in that their peripheral lobes are blunted and shortened where they meet the inner lobes of the outer series. *P. asperum* conforms much more nearly to the definition of a cœnobe as a colony of cells quite similar in form and function.

One might conclude that we have here a simpler type in which cell-differentiation has not yet gone so far as in *P. Boryanum*. I am inclined to the view, however, that in reality *P. asperum* is the more specialized type and expresses more fully the form-determining tendencies which have led to the development of the spines or lobes on the peripheral cells of the colony of *P. Boryanum*.

As we shall find from a study of the method of reproduction in the colony, the cells all inherit alike the tendency to the four-lobed form. This is obvious even in the interior cells of the colony

of *P. Boryanum*. They all show a reëntering angle on their peripheral sides. In *P. asperum* this tendency to the four-lobed form has come more fully to expression, overcoming to quite a degree the adhesion of the cell surfaces so that each cell may assume the form to which its inherited tendencies predispose it. The possible origin of this tendency in the intercellular relations of such groups of cells, I shall discuss later.

In form these intercellular spaces vary from youth to the adult reproductive condition, as will be noted later in discussing reproduction. They also show some degree of variation in different individuals of apparently the same stage of development. In their curved outlines they express very fully the tensions existing in the protoplasm of the cells and the contact relations of the cells in the colony. In colonies with atypical cell arrangement, they may become highly varied in different regions, expressing fully the different and irregular tensions set up in such abnormal or subnormal groupings (Figs. 26-28).

In number, form and position these intercellular spaces form two series, four between the central cell and series II. and ten between series II. and III., the outer series. Of the four intercellular spaces of the inner series two, *a* and *c* (text-fig. 7) lie on the axis of the colony, and the other two, *b* and *e*, are symmetrically placed to the right and left. These four spaces are of three forms and sizes, *a*, the largest, is broadly triangular to shield-shaped (Figs. 5, 6); *c*, the second in size, is roughly an asymmetrical ellipsoid with its greater convexity toward the central cell, and *b* and *e* are still smaller and more or less symmetrical ellipsoids with pointed poles, somewhat lemon-shaped.

The outer series consists of five larger, ovoid to shield-shaped spaces, *i*, *k*, *o*, *t* and *q*, and alternating with them five smaller spaces, *f*, *h*, *j*, *l* and *p*. One of the larger spaces, *q*, and one of the smaller, *j*, are bisected by the axis of the colony. The remaining four of the larger group may be regarded as forming two pairs, a pair, *i* and *k*, symmetrically placed to the right and left of the axis, nearer the *m* pole of the colony, and nearer together than *o* and *t*, the similarly placed pair toward the *n* pole. The remaining four

smaller spaces also form two pairs, *f*, *p* and *h*, *l*, placed as are the larger pairs but with the nearer pair toward the *n* pole of the colony.

In their relation to the cells between which they occur the intercellular spaces form two classes, those formed at the points where three cells come together and where three walls intersect and those formed by retraction of the plane contact walls of two adjacent cells; in other words, the intercellular spaces which are bounded by three cells and those which are bounded by two cells. There are six of the first class, five in the outer series, and one, *a*, in the inner series, and there are eight of the second class, five in the outer series and three in the inner series.

These spaces, as noted, get their outlines and positions from the tendencies of the cells to assume their hereditary four-lobed form and not merely as an expression of surface tension and rounding up such as results in the triangular intercellular spaces in many loose parenchymatous tissues and in the colony of *Gonium*. The final and definite form of each cell in which it differs from its neighbors arises during growth and in irregular colonies these differences may be very marked (Figs. 25-27). They may consist in inequality in the length of the lobes with greater or less blunting of their tips, curving of the lobes, or deformation of the whole trapezoidal outline of the cell till it becomes rhomboidal or some other form. The growth of the cell will result in the protoplasm as flowage and tensions in the direction of the growing lobes and such tensions exerted at four points of the viscous mass will tend to produce a simple catenoidal deformation of the whole such as arises in all semi-fluid, viscous bodies under tension of any sort. Retraction would naturally occur on the surface of contact midway in the regions of tension simulating a tendency of the whole mass to break up into four droplets. The curves bounding the intercellular spaces in the figures (see Fig. 5 especially) are the obvious expression of tensions exerted on the cell mass in the direction of the four lobes. The degree to which this tendency to catenoidal deformation will come to expression will depend on the viscosity of the protoplasm, the adhesion of the cells to each other, etc. It is in these particulars that the species differ and the same species may under varying conditions or at different stages of development differ in such charac-

teristics. There is no question that *P. Boryanum* may at times, and in the same fashion, develop intercellular spaces, though I have never seen them so symmetrically and strongly developed in this species as in *P. asperum*. The production of the general four-lobed outline is, as evidence given below shows, a result of the inherited form of each cell rather than its pressure relations in the colony.

There is further to be considered a certain suggestion of a want of correlation between the form of the cells and their pressure relations in the colonies of *Pediastrum*. Regarding the young cells as equal and rigid globular bodies in one plane, the central cell in a sixteen-celled group would be in contact with and pressed by five cells symmetrically placed about it. Each of the cells of the second series would be in contact with four cells which are not equally spaced about it. The cells of the third series in such a figure would be alternately in contact with one and two cells, corresponding to the contacts of the cells of series III. in the actual colony which are alternately in contact with three and four cells (Figs. 6, 7). If now the globular cell bodies yield to pressure and flatten upon each other, filling the empty spaces in the group, they will (except the central cell) tend to become oblong and four-cornered like the mature cells of *Pediastrum*. On the other hand, *in the commonest form of the thirty-two-celled colonies the central cell is in contact with the six cells of the second series*, and each of the six assumed globular bodies would be in contact with five cells not similarly placed. In the third series of ten, two such globular cells would be in contact with four each, six would be in contact with three each, and two would be in contact with two each. In the outer series fourteen of the fifteen globular cells would be each in contact with one cell, while one would be in contact with two cells, and yet all these cells in both the sixteen- and thirty-two-celled colonies grow into the characteristic four-lobed form with the resulting contact relations found in the mature colony in which in the sixteen-celled colony, for example, the cells of the second series are each in contact with and pressing against six cells and the cells of the outer series are alternately in contact with one and two cells each. The new specific contacts and pressures arising in growth are due to the inherited four-lobed form of the cells, which none

the less, in my opinion, may have arisen in evolution from the pressure and contact relations of the young cells in the common sixteen-celled colony, regarding them merely as surface tension globules. We may conceive, as is described below, that transitorily the young cells at once flatten upon each other and thus give the figure of *P. Boryanum* with no intercellular spaces. The spaces then start to form with the first growth of the young colony in such a fashion as to make the resulting four-lobed cells as nearly isodiametric as is possible with the numbers involved and the inherited tendency to adhere together in the most compact figure possible (groups of three). It is quite conceivable, then, for the sixteen-celled colony, that out of the incompatibilities resulting from the laws of bipartition and surface tension, both operating in the case of an organism whose cells tend to adhere in colonies, the four-lobed form of the cells has been developed from cell forms such as we find in *P. integrum*. It is easy to recognize certain physical stimuli which have been present; first, surface tension tending to keep each cell isodiametric; second, perhaps during growth, functional hypertrophy as we have observed its action in the case of *Hydrodictyon*; third, adhesion tending to keep the contact surfaces plane; fourth, catenoidal deformation, due to growth tension in the direction of the lobes. Each cell is originally like its fellows—a globular or ovoid bit of jelly. Adhesion during the writhing motions of the final stages of the swarming period leads to its being flattened upon its neighbor. This may be favored by low turgor at this period, but we have little evidence on this point. In *P. Boryanum* the cells, as a rule, adhere permanently over their entire original contact surfaces and thus maintain their primary contact relations. In *P. asperum*, however, the surfaces of the cells tend to separate. The degree and location of this separation may be determined by the tendency of the cells to catenoidal deformation as they grow rapidly in the axes of greatest resistance as developed by their four-lobed form. The cells of the whole colony, with the exception of the central cell, are longer in their tangential axes than in their radial axes, since five cells fill the space which six should occupy in the second series of a least-surface group and ten fill the spaces of twelve in the outer series. Surface tension tends in each cell to equalize these two

axes. Taking cell 4 as an example, the pressures upon it are from the cells 1, 3, 11, 12, 13 and 5 and in tending to round up while developing its pressure relations with these cells it forms the wedge-shaped surfaces of contact inclined to each other at the characteristic angles of 120° . The axes of major growth of the cells after the early stages are just what they would be expected to be on the principle of functional hypertrophy, though as shown below, the cells are capable of reaching their typical form even when their contact with other cells has been reduced to a minimum (Figs. 29-33).

The strongly four-lobed cells are in their form adapted to the expression of a typical surface tension configuration for the whole sixteen-celled colony, but this form does not apparently depend for its expression in ontogeny on the contact relations to which it is so perfectly adapted. Whether in phylogeny, as noted, it was not a result of the cellular interactions existing in the colony is, of course, quite another question. The fluctuating variations in the form of the cells and of the intercellular spaces are the direct expression of the effects of functional response to environmental influences operating in ontogeny. But the cell is able independently to develop its fundamentally four-lobed form.

It may be that we have here a case of an adaptive form character which arose in direct response to and as it were determined by environmental factors of cellular interaction which has become so fixed that it is now transmitted in cell division and comes to typical expression without the need of the stimuli of adhesion and pressure relations which originally called it into being. The considerations here developed apply, of course, especially to the sixteen-celled colony. The case of the thirty-two-celled colony will be considered, as noted below, in another connection.

It is during growth that the intercellular spaces are developed. As the cells of the colony reach their mature size the intercellular spaces become again relatively smaller. The cells now increase their volume by expanding in the direction of least resistance, that is, toward the intercellular spaces. As they prepare for reproduction by swarmspore formation this swelling becomes very marked (Fig. 8). The ovoid spaces become triangular, as does the large

space. The spaces between two cells become flattened to thin bi-convex lense-formed figures. This change of form is accompanied by increased density of the cell content, which also becomes more deeply green in color. It appears that the cells are accumulating reserve storage products to be used in the reproductive period. The distinction between this sort of growth and that at the earliest period, when the cells were developing their long lobes and large intercellular spaces, is obvious and parallels the distinction between the periods of growth and of maturing with the accumulation of reproductive reserves in adult many-celled plants and animals.

REPRODUCTION IN *P. ASPERUM*.

Al. Braun ('51) reported De Bary's discovery of the gametes of *Pediastrum* in 1851 and Askenasy ('88) has described their conjugation and shown the similarity of the life history to that of *Hydrodictyon*. Askenasy ('88) shows fully that the final formation of the new colony is essentially the same process when it comes from a zygospore through the polyeder stage and when it is formed directly by asexual reproduction from a cell of a parent colony.

The method of asexual reproduction in *Pediastrum* has been correctly understood since the work of Meyen ('28), who saw the escape of the swarmspores, their free motion and later their combination to form the young colony and Nägeli ('49) correctly concluded that since the number of cells in a colony is regularly a multiple of two the cells must have arisen by bipartition. To be sure, Conn ('08) rather casually describes the swarmspores as continuing to divide after they have come to rest. Whether this statement of Conn's is based on his own observations or is merely an *a priori* guess at what seems to him probable is not clear. Nägeli ('49) in 1849 had already convinced himself to the contrary. There can be no question but that the process of cell multiplication is completed before the swarming period.

I have photographed more or less successfully a large number of colonies with mother cells at various stages of division. There can be no question that here we have a process of successive bipartition of a multinucleated sporeplasm. Smith ('16) has figured from

sections stages showing the cleavage of numerous segments of the sporeplasm and my photographs show the first division, four-cell stage, etc. Smith's figures show clearly that the cells divide by furrows and that regular karyokinetic figures appear in nuclear division. The swarmspore is uninucleated and the sporeplasm becomes multinucleated before cell division begins.

When the colony is to reproduce itself the cells become extremely plump and to some extent lose their deeply four-lobed form (Fig. 8). The spinous projections tend to be drawn in perhaps, though they do not entirely disappear in any of the species. This is well shown in figures of *P. asperum*, 8, 9, and 10, and at a later stage when cleavage is well along in Figs. 11, 12 and 14. These forms would hardly be recognized as belonging to *P. asperum* if it were not possible to find all conceivable intermediate forms between these very turgid types and the immature colonies with slenderly lobed cells, such as are shown in Fig. 6. In such species as *P. clathratum* (Fig. 3) with its very deep sinuses and slender-branched cells it is plain that the four-pointed cell form maintains itself strongly even against the effects of increase of turgor.

As Askenasy ('88) noted, the nuclei are readily recognizable at this stage. Askenasy mentions, but without figures, that the cell division proceeds by a series of successive bipartitions. Figs. 10, *a* and *b*, show the mother cell dividing into two. Cells *c*, *d*, *e* in the same figure show at least the beginnings of the four-cell stages. It is very difficult owing to the density of the cell contents at these stages to bring out the cleavage clearly in photographs, though the furrows are easily visible on focusing. The divisions apparently occur by constriction furrows from the plasma membrane inward as described by Smith ('16), as noted, and by Timberlake ('02) for *Hydrodictyon*. There is no indication of the formation of cell plates, so far as the appearance of the living material is concerned. That we really have constriction furrows forming here and not merely lines of simultaneous cleavage as claimed by Swingle ('97) for *Stypocaulon* and by various authors for a number of fungi (Baum, '00, Kusano, '09, Barrett, '12, Griggs, '12) is suggested by

the rounding up at the edges of the clefts resulting in open furrows over the surface before the cell is completely cut through.

In these plump-celled forms which are about to reproduce the intercellular spaces are much reduced in area and their form is somewhat changed (Figs. 9-14). The cells may, however, reach maturity and divide without becoming so plump as those shown in the cases just noted. In the stage shown in Fig. 13, cleavage is complete and yet the cells are much more deeply lobed than those in Fig. 11, where cleavage has only reached the eight- to sixteen-celled stages.

The study of the living material is very convincing as to the existence here of division by centripetal furrowing, with rectangular intersection of the cleavage planes. The first cleavage plane is regularly in the short axis of the cell (Fig. 10). The successive planes of division cut each other approximately at right angles through the four- and eight-celled stages. In the sixteen-celled and thirty-two-celled stages there are modifications due to the irregular outline of the mother cells. In general, however, the whole series of divisions tends to illustrate the principle of rectangular intersection.

These processes of division as a rule take place during the night, as Smith has noted ('16), and swarming occurs at daylight, or a little later in cool weather. This is also the case in *Hydrodictyon* ('08). By sealing up with hot paraffine an ordinary water mount containing well-grown colonies of *Pediastrum* this rhythm may be readily disturbed. It is probable that the accumulation of waste products is an important factor in such cases. At any rate in preparations sealed up on the previous evening colonies in various stages of division may be found the next day. The division goes on much more slowly under these conditions or may be inhibited all together. I have kept cultures so sealed for long periods without visible deterioration of the colonies. The young colonies may continue to grow for some time, but after the first day or two no cell division occurs. The colonies may be kept alive for six months if they are kept sealed and not allowed to dry out.

The appearance of the mother cell after division is practically

complete is shown in Figs. 12, 13 and 14. Not all the division lines can be brought out in the photograph. The mass is too thick and it is plain that the swarmspores are in at least two layers. In these reproductive stages, when the cells have become very turgid, and especially during the stages of cell division, the mother colonies tend to lose their flatness and become curved and bent in various ways so that it is extremely difficult to get any large number of cells in focus at once. Colonies with cells in which division is complete when freshly mounted at daybreak are liable at any moment to show the beginning of the swarming period. The cells of a colony rarely swarm all at once. As a rule only part of the cells divide in any one night and in the same way there is a succession in the initiation of active movement in the mother cells, suggesting that internal as well as external factors may be concerned in bringing about the active swarming period. When once the swarm cells begin to move, however, the succeeding stages are normally run through with great speed and with no halting. The daughter cells first seem to round up against each other and lose the rectangular outlines which have been maintained by their mutual pressure. Slight twitchings and quiverings can be seen in the mass whose significance is hard to grasp but almost immediately the swarmers begin to glide upon one another and show writhing, struggling movements. The mother cell now bursts by the familiar crescent-shaped slit on its upper or under surface and its contents slide out in the form of a sack or vesicle containing the writhing mass of young swarmspores. This sack, Al. Braun ('51) rightly observed, is the inner layer of the wall of the mother cell. It is elastic and expands to over twice the diameter of the mother cell as soon as it is free. In thus expanding, however, it still maintains the four-cornered outline of the mother cell, as my photographs (Figs. 18-20) show. The two peripheral spinous projections of the mother cell are still recognizable on it as two symmetrically placed papillæ. In the increased space provided by the expansion of the vesicle the movements of the swarmspores become much more active. The writhings become zigzag dashings to and fro. The swarmspores shoot about in all directions through the mass, which has become much looser, and into the open space

around it. This is a perfectly free swimming movement like that at the corresponding stage in *Hydrodictyon*. Oltmanns ('04, p. 194) remarks that the zoöspores probably remain connected by threads of protoplasm but apparently has only Klebs' ('90) mistaken contention as to the corresponding stages in *Hydrodictyon* as the basis for the statement. A single spore can frequently be followed clear through the mass or halfway round its periphery.

This most active swarming period continues for three to four minutes when conditions are favorable. It is followed by a rather sudden slowing down and now the outlines of the future colony appear. The sudden appearance of order out of the chaos of swarming bodies is most striking. The circular outline of the plate appears first and the peripheral cells seem to slow down in their movements, while those in the interior are still quite active. The free-swarming period thus passes over into a second and much longer period of writhing and struggling in which the cells do not move far from their places, but push this way and that between and over each other, crowding and turning around and over without getting completely out of connection with their neighbors as they did in the earlier free-swimming stage. Coincidentally with the slowing down of the movements of the swarmspores they begin to take on the four-lobed form of the adult cells. This change is very conspicuous. The oval swarmspores seem as if they were about to divide into two (Figs. 15-20). Each cell, as the figures show, almost seems to be made up of two pear-shaped halves, the narrowed ends of the halves being the future spines. This sudden assumption by the swarmspores of the four-lobed form is a very striking and conspicuous fact at this stage and is accompanied by rapid growth and mutual pressure between the cells. Walls are formed and the cell contours become more clear cut and definite. All these changes begin with the slowing down of the movements of the swarmspores. The process suggests very strongly the effort of the cells to get into very specific relations with each other and as close together as possible, thus forming the compact plate-shaped colony. As the movement dies away, the behavior of individual cells can be followed with more exactness. A change of position of one cell

apparently may lead to a change of position by all its neighbors and these mutual adjustments and readjustments continue till it seems that a sort of equilibrium is reached. Smith has figured the changes in position of the cells at successive intervals ('16). As noted, the cells in the peripheral series apparently get their definitive positions first, while movement is still quite active in the interior of the young colony. I have not been able to determine just when cilia appear in the swarmspores or when and how they disappear, but doubtless the duration of the active movements of the cells is an index of the limits of the ciliated stage.

To give some hint of the size relations and general appearance of the mother cells and the daughter colonies as they are first formed, I have had reproduced in Figs. 15, 16 and 17 photographs of three stages in the development of a mother cell into a young colony. The difficulties in photographing such stages are very great, as rather long exposures are required and it is not easy to find any considerable number of cells in the same focal plane. Fig. 15 shows the last two cells of a mother colony in which cleavage is complete and swarming is about to begin. All the other cells are already empty and the walls of some of them show faintly. Two young colonies partly out of focus lie nearby. The irregular grouping of the swarmspores in the mother cell shows nothing of the organization of the future colony. There is no evidence of mosaic or any other type of predetermined form inheritance here. In Fig. 16, from a photograph taken a few minutes later, swarming has begun in one of the two mother cells. The vesicle has escaped and lies partly beneath the remaining mother cell. The swarmspores are in active motion and appear only as a gray cloud. It would, of course, require a very short exposure to catch these moving bodies in sharp focus. This figure is less highly magnified than the preceding one and, in all, seven young colonies and part of an eighth are shown lying near, all of them having come earlier from the same parent colony to which the cell just swarming belongs. The figure is printed more deeply, so that the contents of the remaining mother cell appear black, and parts of the outlines of the adjacent empty cells appear more clearly. The attempt was made to focus on the

active mass of swarmspores but the plane of the picture is a little too high and the faintness of the swarming group is partly due to this fact. Fig. 17 is from a plate exposed four or five minutes later. The young colony lies partly beneath the second mother cell but its outlines are in evidence and it is seen to be made up of three concentric rings of cells like the other young colonies lying about. Six of these sister colonies and parts of two more are shown in this figure. The plane of the picture is a little below that of Fig. 16 and other parts of the young colonies are in focus. I have no positive proof of continued ciliary activity in colonies as old as these, but none the less as one watches them they are seen to tip from side to side and even shift their position slightly. Such movements may well be due to slight currents in the water.

As noted, these photographs cannot be regarded as successful, but they give a notion of the relative sizes of the mother cell and the young colony at the time of its birth and the general relations under which the morphogenetic processes take place. With the complete cessation of the movements of its component cells it is obvious at once that the organization of the future colony has been achieved. With the establishment of the peripheral series the young spinous projections are in general all pointing radially outward (Figs. 15-20). In the same way in the inner series, generally speaking, the two-lobed cells have the long axes of their lobes in the radii of the colony viewed as a whole, just as in the full-grown colony. The same exceptions and variations from these rules of orientation can be found in such young colonies as are present in the older ones. The relative number of cells in the outer and inner series, their contacts and the shape of the intercellular spaces are all fixed as they remain throughout subsequent growth and development. Rather rapid growth continues for an hour or so, and with the increase in size of the individual cells their mutual pressure and the development of the intercellular spaces make the specific organization of the colony more conspicuous.

Summarizing, we may distinguish roughly five phases in the vegetative reproduction of *Pediastrum*.

1. Nuclear division which goes on during the vegetative growth of the cells and by which they become multinucleated.

2. Cell division by repeated bipartitions in general according to the principle of rectangular intersections.

3. Escape of the vesicle contemporaneous with quiverings and then slow writhings of the swarmspores for a very brief period, passing at once into

4. The free-swimming stage, lasting several minutes, in which the swarmspores dart about in entire freedom from each other.

5. Slow writhing stage, in which the swarmspores gradually perfect the spatial interrelations found in the adult colony.

The description of reproduction just given may be regarded as representing the process near its optimum as to speed and efficiency. The resulting young colonies (Figs. 15-17) are fairly regular in the arrangement of their cells and rounded in outline. Such conditions are as a rule only achieved in the case of colonies favorably situated and brought under observation only a short time before swarming occurs. In the case of colonies sealed under a cover glass as described above for from six to twenty-four hours before reproduction occurs there are some marked modifications in the process which lead to characteristic changes in the shape of the young colony. One of the commonest deviations from type in the colonies as found in nature is seen in the tendency to be oblong or oval instead of circular in outline. The explanation of this modification in form can be discovered at once by observing the reproduction of colonies which are unfavorably placed. As noted, division and swarming may sometimes be completely inhibited if the colonies are mounted under a cover glass and sealed before they are full grown. If, however, they are about ready to swarm and, for example, are mounted some time in the night before the morning on which they would naturally swarm, the process may take place later in the day. Swarming may thus be delayed for several hours and in such cases it is at once seen that it is less vigorous.

The free-swarming period is shorter or may disappear entirely, the swarmspores only writhing and twisting about without really getting out of contact with each other. The whole active stage is shortened. This may go so far in certain media that the swarmspores scarcely move at all ('88). The fact is to be at once observed in all such cases of a less vigorous and shortened swarming period

that the resulting colonies are never circular in outline but always somewhat elongated in one axis. The spinous projections are less constantly radial in their position and the intercellular contacts and intercellular spaces are far from what I have described above as typical. Photographs of such irregular colonies still inclosed in the mother vesicle are shown in Figs. 18–20. It is difficult, as noted, to bring out the vesicle in a photograph. I have traced over with dilute India ink the outlines of the vesicle in Figs. 18 and 20 to bring out more sharply the points involved. Fig. 19 is left as printed, but the faint outline of the vesicles and their papillæ can be made out. In Fig. 20 an edge view of a young colony in its vesicle is shown. The figures show clearly enough that the long axis of these irregular oblong and oval colonies lies in the long axis of the mother cell. The vesicle, although gelatinous and swollen, is apparently elastic and always maintains the outline of the mother cell even to the retention as noted of two papillæ representing the spinous projections. The conclusion is obvious that these unfavorably situated colonies with reduced activity in swarming are unable to achieve the typical compact circular plate form and the outline of the young colony is influenced by the oblong shape of the enclosing vesicle. The achievement of all the nice adjustments necessary in making a typical least-surface figure requires more effort than the cells of these weakened colonies are capable of and as a result they conform more or less to the outlines of the confining vesicle. Sometimes the result is a flattening of the outline of the colony along one or both edges. Again the result is a more ellipsoidal form. In cases of extreme weakness the colonies may be rather angular (Fig. 23), conforming quite completely to the outlines of the mother cell and, as Askenasy ('88) noted, sometimes not escaping from it. In these extreme cases the colonies are practically always irregular in all their dimensions, with the cells more or less piled upon each other, so that the colony is more than one layer thick. The spinous projections also tend to disappear under these conditions. The effect of environment in modifying and disturbing the morphogenetic processes is thus most clearly shown, and we can class a whole series of such divergences from type as strictly epigenetic and environmental in their origin. The shape and struc-

ture of any given colony of *Pediastrum* conforms to its type in so far as the environment permits. The multiplicity of divergences from the type form for the species is an index of the varying degrees of favorableness in the surroundings of the parent colony and mother cells. The relations of unstable equilibrium between the units of a group of sixteen or thirty-two, as compared with a group of nineteen or thirty-seven, give unusual opportunity for the play of such environmental influences.

FLUCTUATING VARIATIONS IN THE INTERCELLULAR RELATIONS IN THE COLONIES OF *P. ASTERUM* AND *P. BORYANUM*.

The evidence from the above account of asexual reproduction is clear that the colony of *Pediastrum* is formed by the interaction of a group of free-swarming zoöspores without the possibility of any predetermination of its form as such in the arrangement of the parts of the mother cell. A cell can apparently fill any place in the group which forms the young daughter colony. A colony under favorable conditions may attain the rounded outline of a typical least-surface configuration for such a group of cells or under less favorable conditions it may conform more or less wholly to the outline of the mother cell even to the extent of remaining two-layered. I have also described above the general arrangement of the cells and intercellular spaces in a typical adult colony of *P. asperum*, and we may now turn to the question as to the kind and degree of variability which the colonies as they are found in nature exhibit.

In the continuous disk of the typical sixteen-celled colony of *P. Boryanum* I have shown ('16) that the angles of intersection of the cells walls vary considerably in different parts of the colony, the correspondingly placed angles right and left of the axis of the colony tending to be equal. The angles of contact in any fairly typical sixteen-celled colony of *P. asperum* (Fig. 6) are, so far as I am able to determine, quite constantly 120° . The difficulties of measurement here are much greater than in *P. Boryanum*, since the presence of intercellular spaces reduces the surfaces of the cells in contact and the length of the lines by which the angles are measured. Small variations are no doubt quite regularly present, but they are within

the limits of error by any method of measurement I have been able to use. If the ordinary semicircular protractor is used and newly placed for each reading the results show fluctuations of from 1° – 3° between the angles. If, however, the circular protractor with lines marking the angles of 120° is carefully placed so that the three angles can, as it were, be simultaneously read, it is at once apparent how closely the angles approximate 120° , and that the deviations in most cases are so slight as to be practically indistinguishable from appearances due to inequalities in the thickness and density of the cell walls, middle lamellæ, intercellular substances, etc., as shown in the photographs.

TABLE I.
ANGLES OF INTERSECTION OF THE CELL WALLS IN A SELECTED
COLONY OF *P. asperum*.

Points.	Angles.		
	<i>a.</i>	<i>b.</i>	<i>c.</i>
g^1	120°	120°	120°
g^2	122	119	119
g^3	120	120	120
g^4	120	120	120
d^1	120	120	120
d^2	123	120	117
d^3	120	120	120
d^4	120	120	120
d^5	120	120	120
d^6	122	120	118
d^7	121	119	120
d^8	119	120	121
d^9	122	118	120
d^{10}	120	120	120
Totals.....	1689°	1676°	1675°
Av.....	120°	119°	119°

Higher magnifications making the wall lines bounding the angles longer do not essentially help the situation. I have enlarged to a diameter of about 8 cm. the photograph of *P. asperum* (Fig. 6) and carefully and repeatedly measured the angles at each point of contact for the whole colony. The results are given in Table I. The order in which the angles were read is indicated by the lettering *a*, *b*, *c*, at the points g^1 and d . I have not been able in these measurements on *P. asperum* to distinguish between the angles adjacent

to the large and small intercellular spaces, that is, the regions of contact of three and two cells respectively about the points d , d^1 , d^2 , etc., as I did in the case of *P. Boryanum*. Such differences if they are present in *P. asperum* are within the limits of error with the methods of measurement I have so far been able to employ.

The deviations from 120° range from 117° to 123° . The method is not, however, exact and the successive series of measurements from which the averages in the table are derived have little value further than to show plainly enough that the fluctuations here are in most cases relatively slight, and that they appear to range rather equally about 120° for all the cells in the colony.

I have some slight evidence that the inner angle a of the three at the points g^1 , g^2 , etc., and d , d^1 , d^2 , etc., averages a little larger than the other two angles, b and c , but the evidence is by no means adequate on this point and I reserve the data till some further method of testing the questions involved has been devised. It is obvious enough that the fluctuations in the values of these angles of intersection are much less in *P. asperum* than in *P. Boryanum* and this fact is evidently correlated directly with the formation of the large intercellular spaces in *P. asperum*, which permit a curving of the lobes and a general distortion of the whole cell body which results in a more perfect equilibrium between the surface forces at the points of contact of the cells.

The relative degree of conformity to type in a series of the sixteen-celled colonies of *P. asperum* can be better studied by comparing the angles subtended by each cell about the center of the colony. These angles can be measured with more accuracy, and, while they show considerable individual variations, the averages of the rather small numbers obtained show considerable constancy. We may take first a series of fourteen colonies whose cells are arranged in the most common order, namely, one in the center with five around this in the so-called second series and ten in the third or outer series.

It is plain from the table that the bases of the cells of both the second and third series tend to be equal and regarded as arcs of a circle about the center of the colony r (Fig. 7) subtend approximately equal angles. The cells of series II. occupy on the average

TABLE II.

DIMENSIONS OF CELLS IN A SERIES OF FOURTEEN SIXTEEN-CELLED COLONIES OF *P. asperum* AS INDICATED BY THEIR BASES MEASURED AS ARCS OF A CIRCLE ABOUT THE CENTER OF THE COLONY.

Colony.	Cells 2, 3 4, 5 and 6.			
	g^1-g^2 .	g^2-g^3 .	g^3-g^4 .	g^4-g^5 .
294.....	67°	68°	74°	151° ^b
484.....	70	76	68	146
169.....	76	73	74	137
195.....	75	71	74	140
110.....	72	72	76	140
381.....	71	73	71	145
271.....	72	74	65	149
291.....	72	75	70	143
129.....	72	65	73	150
237.....	67	75	73	145
IX.....	76	73	71	140
101.....	72	71	78	139
356.....	66	78	74	142
235.....	74	76	64	146
Totals.....	1003°	1002°	1020°	2013°
Av.....	71°	71°	72°	$\frac{143°}{71°}$

	Cells 7, 8, 9, 10, 11, 12, 13, 14, 15 and 16.									
	d^1-d^2 .	d^2-d^3 .	d^3-d^4 .	d^4-d^5 .	d^5-d^6 .	d^6-d^7 .	d^7-d^8 .	d^8-d^9 .	d^9-d^{10} .	$d^{10}-d^{11}$.
294.....	34°	41°	37°	35°	35°	38°	34°	35°	35°	36°
484.....	34	37	36	38	36	34	36	35	37	37
169.....	36	36	36	39	35	36	34	35	34	39
195.....	35	35	39	37	35	36	34	36	32	41
110.....	36	37	36	37	35	35	38	32	36	38
381.....	34	36	35	37	37	36	36	37	39	35
271.....	40	36	36	40	35	36	33	35	34	35
291.....	38	32	38	37	38	37	32	36	36	36
129.....	39	37	39	33	34	34	35	38	34	37
214.....	36	37	32	36	37	35	34	39	37	37
107.....	33	40	30	38	37	40	38	36	35	33
IX.....	32	38	34	39	36	37	37	37	36	33
101.....	37	34	36	40	36	36	35	35	36	35
356.....	37	35	38	35	40	37	36	35	33	34
235.....	34	32	40	38	39	32	37	38	40	30
Totals.....	535°	543°	542°	559°	545°	539°	529°	539°	534°	536°
Av.....	35.6°	36.5°	36.1°	37.1°	36.3°	35.9°	35.2°	35.9°	35.6°	35.7°

from $71^\circ +$ to $72^\circ +$, 72° being the typical angle for such a group. I have measured the angles occupied by cells 2 and 6, together, as the arc g^1-g^4 which subtends in the average of the fourteen colonies an angle of 143° . Dividing this equally between cells 2 and 6 gives

them each an angle of $71^\circ +$. The smallest angle for any of the cells in series II. in all the fourteen colonies is 64° in colony 235, the largest is 78° in colonies 101 and 356. The range of fluctuating variation is hence in the fourteen colonies 14° or a little less than 20 per cent. of the normal.

The bases of the cells of series III., as the table shows, subtend angles varying in the averages from 35.6° to 37.1° , 36° being the typical angle. The smallest angle in this series is 32° and the largest 41° , a range of fluctuation of 9° . While the number of colonies whose angles have been measured is not large, it seems to me evident from the data that there is a marked tendency to equality in the spaces occupied by the cells in each series and that the typical configurations about which fluctuation occurs would give each of the cells of series II. 72° and each of the cells of series III. 36° . If we arrange the angular measurements of the cells in series II. in a series so as to show the frequency of angles of each particular value, while there are marked irregularities in the series, we have evidence of chance distribution about the value 72° as a mode, 31 angles measuring more than 72° and 29 angles measuring less than 72° (see Table III.). Treating the angles of series III. in the same way we find in spite of fluctuating irregularities 59 angles below the mode at 36° and 58 angles above the mode (Table III.). Here again there is evidence of chance distribution about 36° , the value of the typical angle for such a group with least-surface configuration.

TABLE III.

FREQUENCY OF THE ANGLES OF THE VARIOUS VALUES.

<i>Cells 2-6 Inclusive.</i>														
64°	65°	66°	67°	68°	69°	70°	71°	72°	73°	74°	75°	76°	77°	78°
1	2	1	2	4	2	8	9	10	9	8	7	5	0	2
<i>Cells 7-16 Inclusive.</i>														
30°	31°	32°	33°	34°	35°	36°	37°	38°	39°	40°	41°			
2	0	8	6	17	26	32	25	14	9	8	2			

For *P. Boryanum* I have elsewhere ('16) given the data as to the organization of the colony based on the study of an individual selected for its regularity. The comparison of the type dimensions obtained in this fashion with those obtained from averaging a series

TABLE IV.

VALUES OF THE INCLUDED ANGLES OF THE CELLS OF A SERIES OF SEVEN SIXTEEN-CELLLED COLONIES OF *P. Boryanum* ARRANGED IN THE TABLE AS THEY WERE MEASURED ABOUT THE POINTS g, g^1, g^2 , etc., e, e^1, e^2 , etc., and d, d^1, d^2 , etc.

Colony.	Angles about Point g .		
	$igi.$	$igk.$	$ikh.$
87.....	114°	116°	130°
131.....	115	120	125
1-d.....	122	113	125
1-b.....	108	124	128
39.....	120	120	120
23.....	115	117	128
55.....	111	121	128
Totals.....	805°	831°	884°
Av.....	115°	117°	126°
		Totals.....	117
		Av.....	243°
			121°

Colony.	Angles about Point g^1 .			Angles about Point g^2 .		
	$ig^1i.$	$ig^1k.$	$ig^1h.$	$ig^2i.$	$ig^2k.$	$ig^2h.$
87.....	108°	121°	131°	112°	117°	131°
131.....	100	119	141	107	117	136
1-d.....	108	125	127	96	132	136
1-b.....	115	112	133	107	126	127
39.....	102	136	122	105	120	135
23.....	105	119	136	112	121	127
55.....	113	125	121	102	129	129
Totals.....	751°	857°	911°	741°	862°	921°
Av. right.....	107.2°	122.4°	130.1°	105°	123°	131°
Av. left.....	105.8	131.5	123.1			
Totals.....	213°	253.9°	253.2°			
Av.....	106.5°	126.9°	126.6°			

Colony.	Angles about Point g^3 .			Angles about Point g^4 .		
	$ig^3i.$	$ig^3k.$	$ig^3h.$	$ig^4i.$	$ig^4k.$	$ig^4h.$
87.....	101°	133°	126°	77°	149°	134°
131.....	91	130	139	88	133	139
1-d.....	92	140	128	90	138	132
1-b.....	93	138	129	99	131	130
39.....	86	141	133	91	138	131
23.....	89	136	135	98	135	127
55.....	81	136	142	93	134	132
Totals.....	633°	954°	932°	636°	958°	925°
Av. right.....	90.3°	136.2°	133.1°	90.8°	136.8°	132.1°
Av. left.....	90.8	132.1	136.8			
Totals.....	181.1°	268.3°	269.9°			
Av.....	90.5°	134.1°	134.9°			

TABLE IV.—*Continued.*

Colony.	Angles about ϵ .		
	oeo° .	oek .	keo° .
87.....	152°	96°	112°
131.....	134	120	106
1-d.....	131	105	124
1-b.....	—	—	—
39.....	133	112	105
23.....	129	111	120
55.....	137	108	115
Totals.....	816°	652°	682°
Av.....	136°	108°	113°

Colony.	Angles about ϵ^1 .			Angles about ϵ^2 .		
	oe^1o° .	ke^1eo° .	ke^1eo° .	oe^2o° .	ke^2eo° .	ke^2eo° .
87.....	139°	109°	120°	130°	105°	125°
131.....	146	97	117	136	108	116
1-d.....	132	112	116	120	120	120
1-b.....	—	—	—	—	—	—
39.....	143	113	104	146	111	103
23.....	137	107	116	139	107	114
55.....	132	109	119	145	106	109
Totals.....	829°	647°	692°	816°	657°	687°
Av.....	138°	107°	115°	136°	109°	114°

Colony.	Angles about ϵ^3 .			Angles about ϵ^4 .		
	oe^3o° .	ke^3eo° .	ke^3eo° .	oe^4o° .	ke^4eo° .	ke^4eo° .
87.....	125°	120°	115°	126°	121°	113°
131.....	129	112	119	136	112	112
1-d.....	—	—	—	126	114	120
1-b.....	—	—	—	—	—	—
39.....	140	100	120	130	110	120
23.....	143	103	114	128	114	118
55.....	149	95	116	132	108	120
Totals.....	686°	530°	584°	778°	679°	703°
Average.....	137°	106°	116°	129°	113°	117°
			ϵ^2	137	106	116
			ϵ^1	138	107	115
			ϵ	135	109	113
			ϵ^1	136	109	114
			Totals...	675°	544°	575°
			Av.....	135°	108°	115°

TABLE IV.—Continued.

Colony.	Angles about d^0 .			Angles about d .		
	od^0p .	r^0d^0p .	r^0d^0o .	odp .	rdp .	rdo .
87.....	120°	120°	120°	120°	120°	120°
131.....	105	127	128	109	123	128
I-d.....	99	127	134	118	120	122
I-b.....	—	—	—	—	—	—
39.....	116	116	128	118	115	127
23.....	102	118	139	119	120	121
55.....	109	129	122	109	126	125
Totals ...	651°	737°	771°	693°	724°	743°
Av.....	108.5°	122.8°	128.5°	Right..... 115.5° Left..... 108.5°	120.6° 122.8°	123.8° 128.5°
				Totals..... 224°	243.4°	252.3°
				Av..... 112°	121.7°	126.1°

Colony.	Angles about d^0 .			Angles about d^1 .		
	od^0p .	r^0d^0p .	r^0d^0o .	p^1d^1o .	r^1d^1p .	r^1d^1o .
87.....	108°	123°	129°	—°	—°	—°
131.....	114	120	126	105	126	129
I-d.....	98	132	130	106	126	128
I-b.....	—	—	—	—	—	—
39.....	116	118	126	120	120	120
23.....	120	113	127	116	120	124
55.....	107	128	125	113	120	127
Totals ...	663°	734°	763°	560°	612°	628°
Av.....	110.5°	122.3°	127.1°	Right..... 112° Left..... 110.5°	122.4° 122.3°	125.6° 127.1°
				Totals..... 222°	244.7°	252.7°
				Av..... 111°	122°	126°

Colony.	Angles about d^1 .			Angles about d^2 .		
	od^1p .	r^1d^1p .	r^1d^1o .	od^2p .	r^2d^2p .	r^2d^2o .
87.....	111°	120°	129°	102°	131°	127°
131.....	111	122	127	103	127	130
I-d.....	—	—	—	87	131	142
I-b.....	—	—	—	—	—	—
39.....	116	124	120	117	128	115
23.....	—	—	—	100	127	133
55.....	97	129	134	112	124	124
Totals ...	435°	495°	510°	621°	768°	771°
Av.....	108.7°	123.7°	127.5°	Right..... 103° Left..... 108	128° 123	129° 127
				Totals..... 211°	251°	253°
				Av..... 105°	125°	127°

TABLE IV.—*Continued.*

Colony.	Angles about d^b .			Angles about d^b .		
	$d^b d^b p^b$.	$r^b d^b p^b$.	$r^b d^b d^b$.	$p^b d^b d^b$.	$r^b d^b p^b$.	$r^b d^b d^b$.
87.....	110°	122°	128°	90°	139°	131°
131.....	90	128	142	105	125	130
1- d	—	—	—	100	131	129
1- b	—	—	—	—	—	—
39.....	112	127	121	101	123	136
23.....	—	—	—	—	—	—
55.....	112	125	123	104	123	133
Totals ...	424°	502°	514°	496°	641°	659°
Av.....	106°	125.5°	128.5°	Right.....100°	128°	131°
				Left.....106	125	128
				Totals.....206°	253°	259°
				Av.....103°	126°	129°

Colony.	Angles about d^b .			Angles about d^b .		
	$d^b d^b p^b$.	$r^b d^b p^b$.	$r^b d^b d^b$.	$d^b d^b p^b$.	$r^b d^b p^b$.	$r^b d^b d^b$.
87.....	105°	129°	126°	100°	131°	129°
131.....	114	126	120	105	128	127
1- d	—	—	—	108	126	126
1- b	—	—	—	—	—	—
39.....	111	117	132	104	127	129
23.....	—	—	—	—	—	—
55.....	114	120	126	108	129	123
Totals ...	144°	492°	504°	525°	641°	634°
Av.....	111°	123°	126°	Right.....105°	128°	126°
				Left.....111	123	126
				Totals.....216°	251°	252°
				Av.....108°	125°	126°

of selected individuals is made possible with the data given below in Table IV. The lettering of the angles, etc., as noted above, is given in Fig. 35 which is taken from my earlier paper ('16, Fig. 1b).

The comparison of the values of the included angles made by the intersection of the cell walls in two such types as *P. Boryanum* and *P. asperum* brings out very clearly the significance of the cell form as related to the symmetry of such groups. As noted in *P. Boryanum* the angles fluctuate widely, while in *P. asperum* their variations are almost entirely within the limits of error in measuring them.

The data given in Table IV. are based on measurements of seven colonies of *P. Boryanum*, all of which again have the common arrangement of their cells, that is, one cell in the center, five in the second series, and ten in the third series with the long lobes of the cells of series II. and III. directed radially outward. The lettering of the angles, etc., is given as noted in the type diagram. These seven individuals are all relatively regular and symmetrical and the angles of intersection of their cell walls do not fluctuate so widely as is the case in colonies whose cells are more irregularly placed (Figs. 26-28). It seems, however, impossible to include these more irregular colonies with the more symmetrical types in a comparison of the values of the included angles of their cells, since, as I have pointed out already, the typical colonies tend to be bilaterally symmetrical and a comparison of fluctuation in the included angles of their cells can only be of significance if made between correspondingly placed angles (homologous angles of Rhumbler ('02)). In the irregularly arranged colonies it is quite impossible to compare angles as similarly placed with reference to the pressure relations in the colony. In the case of these irregular colonies I have brought together the values of the included angles of all their cells and classified them according to their value in degrees without reference to their specific positions in the colony. The data so obtained will be briefly discussed later. The seven colonies whose angles are here compared are a selected group and the figure which is obtained by averaging their values we may call for convenience the diagram of the average of the common type. I have not drawn this figure as a larger number of measurements is needed to give such a drawing fundamental significance. The reëntering angles of the cells and our lack of quantitative knowledge of the adhesion and viscosity of the protoplasm make it impossible to compute a theoretical type configuration of sixteen units in such a group which might be made a standard of comparison. The figure derived from averaging the corresponding elements in an exceptionally regular individual as given in my earlier paper we may similarly call the type diagram from a selected individual. The significance of the measurements of such a series of fairly regular colonies may be best discussed in connection with the measurements of the single colony selected for its symmetry.

In Table V. I have brought together the average values of each of the included angles of the cells arranged as right and left pairs and the averages of these pairs in comparison with the corresponding measurements of the selected colony No. 55 which I gave as noted in a former paper ('16, pp. 98, 99).

The table, section I, gives in order the values of each of the five included angles of the central cell and of the included angles of the cells of series II. and III. in these seven colonies arranged in right and left pairs and averaged. In the right-hand column are the corresponding values for the selected colony, No. 55. For convenience we may call the unpaired angle of the central cell, igi^s , the basal angle. The right and left pair of angles ig^1i^1 and $i^3g^3i^3$ the lateral angles, and the remaining pair which measure the two lobes of the cell ig^2i^3 and $i^4g^4i^5$ the apical angles. In the cells of series II. (except cell 4) we shall have two basal, two lateral and two apical angles and in cell 4 and in all the cells of series III. three basal angles, for example, in cell 12 $p^4d^4r^4$, $p^5d^5r^5$, and $p^4h^3p^5$ and in cell 4 the corresponding three angles.

In the central cell the unpaired angle igi^s on the axis of the colony is the largest of the five in both cases. It is 115° for the average of the series and 111° for the single colony. The apical pair of angles bounding the tips of the lobes $i^1g^2i^3$ 90° and $i^4g^3i^5$ 90° are the smallest of the five. Their values are nearly equal in the averages from the series, as they should be for the bilateral symmetry of the colony. In the single colony, No. 55, they are markedly unequal, 81° and 93° , though their average, 87° , is only three degrees different from the average of the series 90° .

The average values of the lateral angles ig^1i^1 107° and ig^3i^3 105° are intermediate between those of the basal and apical angles of the cell in the averages of the series as they also are in the single colony. In the latter again they differ by 11° though their average, 108° , differs by only 2° from that of the series, 106° . On the whole, the differences between the typical shape of the central cell as determined from the selected individual and as determined by the average of a selected series are within the range of errors in measurement by the methods used for angular dimensions in photographs of such objects.

TABLE V.

AVERAGE VALUES OF EACH OF THE INCLUDED ANGLES OF THE CELLS AND AVERAGES OF THE RIGHT AND LEFT PAIRED ANGLES IN A SERIES OF SEVEN 16-CELLED COLONIES OF *P. Boryanum* COMPARED WITH THE CORRESPONDING ANGLES IN THE SELECTED TYPE DIAGRAM. ('16 pp. 98, 99.)

1. Includes Angles of the Central Cell.

				Average.	Type diagram.
$i^1g^1i^1$	115°			115°	111°
$i^1g^1i^1$	107°	$i^1g^4i^1$	105°	106°	108°
$i^1g^2i^1$	90°	$i^1g^2i^1$	90°	90°	87°

2. Basal Angles of Cells 2-6.

igk	126°	i^1gk	117°	121°	124.5° 126° 134° 138°
ig^1k^1	122°	$l^1g^1k^1$	131°	126°	
$i^1g^1k^1$	130°	$i^1g^1k^1$	123°	126°	
$i^1g^2k^2$	136°	$i^1g^2k^2$	132°	134°	
$i^1g^2k^2$	133°	$i^1g^2k^2$	136°	134°	
Totals.....	647°		639°	641°	
Av.....	129°		127°	128°	

3. Lateral Angles of Cells 2-6.

keo	108°	keo^3	113°	110°	111° 107° 120°
$k^1e^1o^1$	114	$k^1e^1o^1$	107°	110°	
$k^1e^1o^2$	109	$k^1e^1o^1$	115°	112°	
$k^1e^1o^3$	117	$k^1e^1o^1$	106°	111°	
$k^1e^1o^4$	113	$k^1e^1o^1$	116°	114°	
Totals.....				557°	338°
Av.....				111°	112°

4. Apical Angles of Cells 2-6.

odp	115.5°	$o^3d^3p^3$	108.5°	112°	108° 108°
$o^1d^1p^1$	112.0	$o^3d^3p^3$	110.5	111.2	
$o^1d^1p^2$	103.0	$o^1d^1p^1$	108.7	105.8	
$o^1d^1p^3$	100.0	$o^3d^3p^3$	106.0	103	
$o^1d^1p^4$	105.0	$o^3d^3p^3$	111.0	108	
Totals.....	535.5°		544.7°	540.0°	
Av.....	107.1°		108.9°	108°	

5. Mid-basal Angles of Cells 7, 9, 11, 13 and 15.

$o^2e^1o^3$	136°			136°	137° 133°
$o^1e^1o^3$	136	$o^1e^1o^3$	138°	137	
$o^1e^1o^4$	129	$o^1e^1o^3$	137°	133	

TABLE V.—Continued.

6. Basal Angles of Cells 7-16.

pdr	120°	$p^3d^2r^3$	122°
$p^1d^1r^1$	122	$p^3d^2r^3$	122
$p^2d^2r^2$	128	$p^1d^1r^1$	123
$p^3d^3r^3$	128	$p^4d^4r^4$	125
$p^4d^4r^4$	128	$p^3d^3r^3$	123
Totals	626°		615°
Av.	125°		123°
odr	123°	$o^3d^3r^3$	128
$o^1d^1r^1$	125	$o^3d^3r^3$	127
$o^2d^2r^2$	129	$o^1d^1r^1$	127
$o^3d^3r^3$	131	$o^4d^4r^4$	128
$o^4d^4r^4$	126	$o^3d^3r^3$	126
Totals	634°		636°
Av.	126°		127°

The basal angles of the cells of series II. igk , i^3gk , ig^1k^1 , $i^3g^4k^4$, etc., also constitute five pairs of correspondingly placed angles right and left of the axis of the colony mn . The average values of each for the series of seven colonies are arranged in corresponding pairs in the table, section 2. In this series the average values of the right and left pairs are seen to be progressively smaller as we pass in the direction from pole n towards pole m in the colony. The values range from 121° in the first pair about the point g to 134° in the pairs about g^2 and g^3 . The equivalence of the adjacent basal angles of cells 2-3, 126°, and 3-4, 134°, is to be expected as a characteristic of the type configuration though it is more or less accidental doubtless that it should appear on the basis of so few measurements. The progressive increase in size of the basal angles of these cells is correlated with the reduction in value of the corresponding included angles of cell 1 proceeding from basal to lateral and apical angles. As shown in the table, column 4, the values of the corresponding angles in the selected type diagram from colony 55 agree fairly well with these averages from the seven colonies. The first pair are smaller in the average from the series. The next three pairs are the same, and the last pair, the basal angles of cell 4, are smaller in the average type than in the selected type.

We have two sets of points of intersection between the walls of the cells of series II. and series III., due to the fact that there are ten cells in series III. to five cells in series II. We may consider first the included angles of cells 2-6 about the five points of intersection marked ee^1e^2 , etc. The values of these angles for the seven colonies and their averages are given in Table IV. Point e is on the axis. The remaining four points, e^1e^4 , are placed symmetrically right and left of the axis nm as is indicated by their position in the table. The average values of the lateral angles of cells 2, 3, 4, 5, and 6 about these points e , e^1 , etc., are arranged in five corresponding right and left pairs in Table V., section 3.

There is no adequate evidence of any regularly progressive change in value in the averages of these five pairs as compared with the progressive change in value of the basal angles of these cells. This is doubtless owing to the increased distance of these angles from the five-sided central cell with its unequal included angles, due to its inherited form tendencies. There is a manifest tendency for the angles of intersection of the cell walls to become equal in harmony with the general symmetry of a least-surface configuration. The values of these angles from the averages of the series agree fairly well with the values of the corresponding angles in the selected type figure. In the case of the lateral angles of cell 4, an arbitrary value, 120° , was assigned in the diagram. The actual average value of these angles in colony 55 was 112° , as shown in the table ('16, p. 98), and this is only two degrees from the average value of these angles in the series of seven colonies.

The values of the right and left pairs of the apical angles of cells 2-6 are given in Table V., section 4. There is considerable fluctuation in the values of these angles but the average of the series, 108° , agrees closely with the value obtained for the same angles in the selected colony 55. In this case again an arbitrary value (100°) was given to the apical angles of cell 4 in the type diagram and the average for the series agrees with the measurements from the selected colony, 109° , and not with the arbitrarily assigned value.

There is no clear evidence from the series that there is any progressive change in value of these apical angles odp , $o^1d^1p^1$ of the

cells of series II. as we pass from pole n to pole m of the colony. The average values of these angles, comparing all seven colonies, have an extreme range of 9° from 103° to 112° , with, as noted, an average of the averages for all the colonies of 108° . In the single colony, No. 55, the range of variation was 17° from 97° to 114° . Colony No. 87 showed a range of variation of 30° from 90° to 120° in the values of the angles odp , $o^1d^1p^1$, etc.

The average values of the five mid-basal angles of cells 7, 9, 11, 13 and 15 are given in Table V., section 5. We have here a case in which the average values of the angles in the series of seven colonies is the same as the value (133°) arbitrarily assigned in the selected type diagram for the mid-basal angles of cells 11 and 13, and differs by seven degrees from the average value as measured (140°) of these two angles in colony 55, from which the selected type diagram was derived. This is the reverse of the result as we have found it in the other two cases noted above and a fourth case noted below in which an arbitrary value was given to angles in the selected type diagram. In the three other cases the average value of the angles in colony 55 as measured is nearer to the average value of the corresponding angles in the series of seven colonies than to the arbitrarily assigned value. As I have already pointed out ('16), the angles about the point e^3 in colony 55 are obviously to the eye the most unsymmetrical and aberrant in the whole colony and the possibility of making consistent arbitrary corrections for these asymmetries and their correlated effects on the other angles in the region is not very great. The values of the unpaired angle oeo° and the pair at e^1 and e^4 agree closely with those obtained from the selected colony No. 55 and given in the selected type diagram. The values of these mid-basal angles of the peripheral cells are larger than those of the other angles of the groups about the points of intersection e , e^1 , e^2 , etc., and this we may regard as a direct correlative of the fact that the tangential diameters of the cells of series II. and III. are regularly greater than their radial diameters. If this tangential elongation of the cells were directly determined by the fact that there are but five cells in series II. and ten cells in series III., instead of six and twelve, the normal numbers for a least-surface configuration in which all three angles would be 120°

each, we might be able to give a fixed value to this relation between the inequality of the diameters and the inequality of the angles about e and to get some notion of the viscosity of the protoplasm, the adhesion of the cells to each other, etc. *As noted, however, it is obvious that the inequality of the diameter may exist in some degree at least in approximately free cells, as is shown in figures 29-33.*

In the basal included angles of cells 7, 8, 9, 10, etc., of series III., we have two series consisting of five pairs each placed symmetrically right and left of the axis mn of the colony, as in the case of the corresponding angles, about gg^1 , etc., and ee^1 , etc. The value of each of these angles for each of the seven colonies is given in Table IV. The averages arranged as two sets of corresponding right and left pairs are given in Table V., section 6. The agreement in the values of the averages of these sets is rather close, the range being from 123° , the smallest, to 127° , the largest. It seems probable that in the type configuration determined by surface tension and the inherited shape of the cells these angles tend to be equal. The average for the different sets is:

For the Series.	Type Diagram.	Colony No. 55.
125°	127°	127°
123°	123°	123°
126°	130°	130°
127°	131°	123°
Total.....501°	128°	128°
Av.125°	635°	631°
	127°	126°

In the selected type diagram derived from the selected colony, No. 55, the average for these angles is 127° . The colony No. 55 is, however, especially irregular in the region of cell four, and an arbitrary value, 131° , was assigned to the two angles $o^4d^4r^4$ and $o^5d^5r^5$. If the measured value for these two angles, 123° , is taken instead of the arbitrary value, the average of these angles for the single selected colony, No. 55, becomes 126° , only 1° different from that for the series.

On the whole, the values for the included angles of the cells agree fairly well when derived by averaging the corresponding

pairs in a series of colonies of similar cell arrangement with those derived by averaging the values of the corresponding pairs of angles in a colony selected for its obvious symmetry.

I have emphasized the difficulty of measuring the angles in photographs of such small objects with the lack of sharpness in the cell walls, especially at points of intersections, etc. Only approximations can be achieved with the technique I have used. The fact that the colonies are not absolutely flat figures so that the plane of the photograph cuts the colony at different levels and the further fact that the walls are not absolutely vertical to the plane of the colony present difficulties inherent in the nature of the material.

The average values of the angles measured from the center of the colony which the corresponding cells in the series of seven colonies subtend are given in Table VI. The exact determination of the center of the colony is not easy in view of the irregularities of its boundaries. The point taken as the center in each colony was midway between the point of intersection of the major axes of the colony and the point of intersection of the major axes of the central cell. The values obtained from averaging the series like those for the single selected colony No. 55 and those of the corresponding angles in *P. asperum* (Table II.) are fairly close to 36° , the angle for a strictly surface tension configuration. There can be little doubt that these angles tend to be equal as would be expected were surface tension and adhesion alone operative.

TABLE VI.

DIMENSIONS OF CELLS 7-16 IN A SERIES OF SEVEN COLONIES OF *P. Boryanum*
AS INDICATED BY THEIR BASES MEASURED AS ARCS OF A CIRCLE
ABOUT THE CENTER OF THE COLONY.

Colony.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.
87.....	38°	30°	40°	35°	37°	30°	38°	36°	35°	41°
131.....	37	35	35	36	36	36	36	36	37	36
1a.....	35	37	35	37	36	38	34	34	37	37
1b.....	—	—	—	—	38	34	38	33	36	38
34.....	35	35	39	32	37	40	36	35	36	35
23.....	37	37	37	32	41	34	41	28	40	33
55.....	35	36	34	36	36	38	36	36	35	38
Totals....	217°	210°	220°	208°	261°	250°	259°	238°	256°	258°
Av.....	36°	35°	36°	34°	37°	35°	37°	34°	36°	36°

How much significance can be attached to the degree of agreement obtained by the two methods used in obtaining the norms of all these fluctuating elements can only be determined by more extensive statistical studies both of especially symmetrical single colonies and extensive series of colonies chosen only on the basis of their having a similar arrangement of their cells. The tendency to equality shown in the values of the corresponding angles both for the intersection of the walls and for the spaces occupied by the entire cells certainly suggests that the structure of the colony tends to be a least-surface configuration with all angles of intersection of the cell walls equal to 120° and all the cells subtending equal angles about the center of the colony, this tendency being in every case limited, however, by the inherited form of the cells and the accidents of environment.

The results of my measurements of the homologous angles in the colonies of *Pediastrum* are in agreement with Rhumbler's ('02) results obtained by measuring the homologous marginal angles of various Foraminifera and confirm still further the conception of the semi-liquid nature of plant and animal protoplasm. Rhumbler uses these results primarily as evidence on this point. The fact that only homologous angles tend to be equal leads him at once, however, to emphasize the heterogeneity in structure of the protoplasm resulting in an anomogenous consistency and anomogenous tensions in different regions of the cell. The cell of *Pediastrum* with its inherited four-lobed form operating always with surface tension in determining the value of any given cell angle is also a notably anomogenous system, as compared with a simple fluid droplet. In the morphogenesis of the colony it is obvious that this anomogeneity is quite as important a factor as is the principle of surface tension. It is in the indisputable evidence from both Rhumbler's material and my own of the interplay of capillarity, protoplasmic anomogeneity, and especially of the principle of binary fission that we get a basis for interpreting the complexity of the form elements with which we are confronted even in such simple organisms as the Foraminifera and cœnobic algæ. The least-surface configuration comes to expression in *Pediastrum* in so far as is consistent with the inherited cell form and consistency and with

cell numbers produced by bipartition. The endless variations in form found on comparing a series of colonies are the expression of the unstable equilibrium, arising especially from the simultaneous operation of the law of bipartition and the physical principle of least surfaces.

In the series of colonies chosen I have included as noted only individuals with the common plan of $1 + 5 + 10$, since it is impossible to compare the angles fairly in individuals with different geometric plans. This is obvious in the case of the superficially

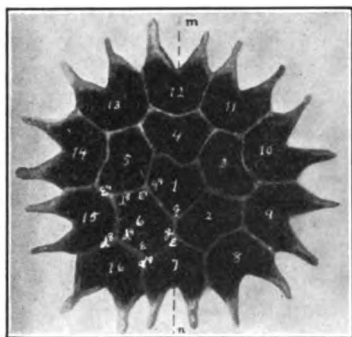


FIG. 25. *Pediatrum Boryanum*. Colony with cell number 6 so displaced that the side which should be adjacent to cell 5 is in contact with cell 1, the side that should be in contact with cell 1 is in contact with cell 2, etc. The remainder of the cells are normally placed. \times about 600.

rather regular colony numbered 67 (Fig. 25). In this colony all the cells are regularly and symmetrically placed except No. 6, in series II. This cell has swung around until its major axes, both radial and tangential, are displaced about 45° . Its reëntering angle normally under the middle of cell 16 is now under cell 15. The entire cell has been, broadly speaking, rotated through one sixth of its circumference so that each of its sides has been displaced by one in its relations with the sides of the neighboring cells. The side normally adjacent to cell 5 is now adjacent to cell 1. The side normally adjacent to cell 1 is now adjacent to cell 2 and much reduced in length. The side normally adjacent to cell 2 is now adjacent to cell 7, etc. Cells 15 and 7 have slipped in toward the center of the colony so that its peripheral outline has been flattened

at these points. The central cell is more nearly isodiametric, etc. In such a colony it is plain that the included angles of cell 6, and those of all its immediate neighbors at least, are under quite different pressure relations than they would be with the normal cell arrangement. Their fluctuations will be of a different order than if they were normally placed. The writhing, struggling motions of the final stage of swarming as described above could only have resulted in the normal relations of equilibrium in case they had been of sufficient violence to bring the cell out of its present abnormal relations into the normal so that the properly matched sides of it and its neighbors would be in contact.

The cell has reached a condition of equilibrium in its pressure relations with the adjacent cells, but this equilibrium has not achieved anything like equivalence in value or position for the corresponding sides and angles. The palpable asymmetry in this cell 6 and its neighbors is most convincing proof that the form of the cell is not influenced merely by its pressure relations in the colony, but also by its inherited tendency to assume the characteristic four-lobed outline. The displacement of cell 6 is brought out very clearly by comparing the right and left pair of cells 3 and 5 with the right and left pair 2 and 6. In spite of fluctuating variations cell 3 could be superimposed on cell 5 by merely rotating it on the axis of the colony *mn* through an angle of 180° . Whereas to superimpose cell 2 on cell 6 there would be necessary a further rotation of No. 6 about its center and in the plane of the colony through about 45° so as to bring the corresponding sides and angles of the two cells together.

Colony 67 illustrates asymmetry originating in the displacement of a single cell to the extent of bringing unmatched sides together. This we may call anomogenous asymmetry as contrasted with the asymmetries involving merely fluctuation in the values of sides and angles without the passing of a critical point which alters the fundamental arrangement of the cells by bringing about abnormal juxtapositions of sides and angles.

All grades and degrees of this anomogenous displacement of cells can be found in nature. Two general types of irregularity can be distinguished. The first is an irregularity which does not pri-

marily affect the outline of the colony or the arrangement of the cells in concentric series about a center, the displacement being largely in the position of the major axes of the individual cells. This is illustrated as noted in colony 67 (Fig. 25). The second results in an abnormal form for the colony as a whole and the loss of the concentric arrangement of the cells (Figs. 26 and 28). The two types are more or less combined, of course, in the majority of cases.

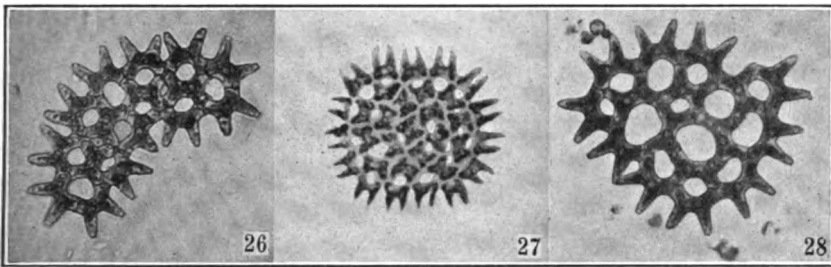


FIG. 26. *Pediatrum asperum*. Colony irregular, crescent-shaped form. \times about 425.

FIG. 27. *P. asperum*. Colony fairly regular in outline but interior cells very irregularly placed. \times about 275.

FIG. 28. *P. asperum*. Irregular colony, somewhat triangular in outline. \times about 425.

The most extreme case of the first type which I have observed is seen in the thirty-two-celled colony (Fig. 27). Here almost all the interior cells are anomogenous in their position and interrelations with their neighbor cells, though there is the common general arrangement for a thirty-two-celled colony; one in the center, six cells in series II., ten cells in series III., and fifteen cells in series IV. All the cells of the outer series are normally placed with long spines outward and the general outline of the colony is circular, but the interior cells are in absolute confusion, as compared with the typical arrangement. Only three cells of series III. have their long lobes radially outward and their long axes tangential and these three are not in normal contact relations with the cells of series II. This colony emphasizes the existence of the stage described under the head of reproduction, where it was noted that the cells of the peripheral series seem to get their definitive positions first while the

interior cells are still actively swarming. The appearance here is as if the development of the colony had proceeded normally until the peripheral cells had gotten their places and then for some reason activity was checked before the interrelations of the cells in the interior had been worked out. It would be possible to express all this confusion in degrees of displacement of the major axis of each cell, but the situation is sufficiently clear from a comparison of this colony with that shown in Fig. 4 without giving it such a mathematical expression. I shall include data on this point in a later study from a wider comparative viewpoint involving the general effect of increasing numbers of cells on the organization of the colonies.

An extreme of irregularity of the second type which is expressed in the general contour of the colony is shown, as noted above, in Fig. 26. Here the colony is crescentic in outline. The type arrangement of cells for a sixteen-celled colony has entirely disappeared and we can no longer recognize a central cell with two concentric series about it and yet the inherited form of the cells is quite perfectly developed in all cases. The modifications are such as are obviously due to the special pressure relations under which each cell finds itself. It is possible, of course, in many cases to identify all the angles of any particular cell and to combine them in homologous groups for the colony and a whole series of colonies, as I have done for the series of more regular individuals. But in these irregular colonies the major axes of the colony are frequently quite unrecognizable and any particular included angle of a cell will be so obviously misplaced and with such unusual pressure relations that the comparison of its values in different colonies becomes a very complex problem.

I have brought together in Table VII. the values of all the included angles in a series of both regular and irregular sixteen-celled specimens of *P. Boryanum*. The values are given for groups differing by three degrees. The data could, of course, be represented graphically in a curve, but the main point illustrated is brought out quite well from a glance at the figures. They form a series culminating in 120° and ranging somewhat similarly above and below this number. The total number of angles with greater value than

TABLE VII.

FREQUENCIES OF THE ANGLES OF VALUES BETWEEN THE EXTREME 86° AND 176°
IN A SERIES OF THIRTEEN COLONIES OF *P. Boryanum* TAKEN BY CHANCE.
THE VALUES ARE GROUPED BY THREES.

	86° to 88°	89° to 91°	92° to 94°	95° to 97°	98° to 100°	101° to 103°	104° to 106°	107° to 109°	110° to 112°	113° to 115°	116° to 118°	119° to 121°
No. of angles.....	1	3	2	2	5	3	14	26	33	42	44	121
	122° to 124°	125° to 127°	128° to 130°	131° to 133°	134° to 136°	137° to 139°	140° to 142°	143° to 145°	146° to 148°	150°	155°	176°
No. of angles.....	98	61	39	15	6	4	4	1	2	1	1	1

120° is 252. The total number which have a value less than 120° is 189. The number recorded for 120° is perhaps unduly large. Since, as I have noted, it is quite impossible to judge within one or two degrees with any certainty there is perhaps a tendency to assign too frequently an angle of 120° rather than 119° or 121° . On the other hand, it is not impossible that the angle 120° being the point of equilibrium in the surface tension group, there may be some especial fixity in the configuration when it is once achieved, so that when it arises by chance as a result of the more protracted slow writhing movements of the final stage in forming the colony, it may be maintained in a certain number of points of intersection at the expense even of greater inequalities at other adjacent points. When once attained exactly it may be more persistent than any other angular value. But whether or not the number of angles with a value of 120° is correctly determined there is no question as to the general tendency in these angles to fluctuate about 120° as a center or modal point. On the other hand, it would be quite inadmissible in the light of the results obtained by comparing the corresponding angles of a series of colonies with similar arrangement (Table V.) or a single colony selected for its symmetry ('16, p. 98) to conclude that the type colony of *P. Boryanum* should have all its included angles equal to 120° . With sufficiently large numbers of cases the secondary modal points representing the special values of the included angles of the central cell, etc., should emerge.

The average values for the corresponding sides of the cells in

TABLE VIII.
LENGTH IN MM. OF THE CELL BOUNDARIES IN A SERIES OF SIX
COLONIES OF *P. Boryanum*.

Sides of Central Cells.

Colony.	<i>i.</i>	<i>i</i> l.	<i>i</i> ².	<i>i</i> ³.	<i>i</i> ⁴.	<i>i</i> ⁵.
87.....	8	7	4.5	5	9	7.5
131.....	9	7	4.5	5.5	7.5	9
1-d.....	11	9	7	6.5	10.5	12
39.....	7.5	9	4.5	4.5	9	7.5
23.....	8.5	9.5	4.5	4.5	8	8.5
55.....	9.5	9.25	6	5	8.75	10.5
Totals.....	53.0	50.7	31.0	31	54.75	55.0
Av.....	8.8	8.4	5.1	5.1	9.1	9.1

Radial Walls of the Cells of Series II.

	<i>k.</i>	<i>k</i> l.	<i>k</i> ².	<i>k</i> ³.	<i>k</i> ⁴.
87.....	7.5	7	7	5	6.5
131.....	7	7	7	6.5	7.5
1-d.....	10	8	9.5	9.5	9.5
39.....	9.5	7.5	8	7	8
23.....	7	6.5	5	5.5	6
55.....	8	9.0	6.5	8.5	8
Totals.....	49.0	45.0	43.0	42.0	45.5
Av.....	8.1+	7.5+	7.1+	7+	7.5

Basal Walls of Cells 7, 9, 11, 13 and 15.

	<i>o.</i>	<i>o</i> l.	<i>o</i> ².	<i>o</i> ³.	<i>o</i> ⁴.	<i>o</i> ⁵.	<i>o</i> ⁶.	<i>o</i> ⁷.	<i>o</i> ⁸.	<i>o</i> ⁹.
87.....	7	6.5	6.5	5.5	6.5	6	7	5.5	6.5	4
131.....	4.5	5.5	5	6	5	4.5	5.5	5.5	5	6
1-d.....	7.5	9	7	7	7	6	7	7	7	8
39.....	5.5	6	6	6	5.5	5.5	7	6.5	5.5	6
23.....	5	6.5	6	6.5	5.5	5.5	5	5.5	6	5.5
55.....	7.5	6	6.5	7	7	4	8	7	7	6
Totals....	37.0	39.5	37.0	38.0	36.5	31.5	39.5	37.0	37.0	35.5
Av.....	6.1	6.5	6.1	6.3	6	5.2	6.5	6.1	6.1	5.9

Radial Walls of Series III.

	<i>r.</i>	<i>r</i> l.	<i>r</i> ².	<i>r</i> ³.	<i>r</i> ⁴.	<i>r</i> ⁵.	<i>r</i> ⁶.	<i>r</i> ⁷.	<i>r</i> ⁸.	<i>r</i> ⁹.
87.....	6.5	7	7	7	6.5	7	7.5	7	7	7.5
131.....	7.5	7.5	7.5	8	7	8	7	8	7.5	7
1-d.....	8	8	8.5	9	8.5	8		8.5	8.5	7
39.....	7	8	7	8	9	9	8	8.5	8	7.5
23.....	8.5	7	7	7.5	8	8.5	7	7.5	8.5	8
55.....	9.5	10	9.5	8	8.5	9	8.5	8	9	9
Totals....	47.0	47.5	46.5	47.5	47.5	49.5	38.0	47.5	48.5	46.0
Av.....	7.8	7.9	7.7	7.9	7.9	8.2	7.6	7.9	8	7.6

the series of seven colonies of *P. Boryanum* are given in Table VIII., and agree well with those obtained for the selected colony ('16, p. 98). I have not included measurements of the basal walls of cells 8, 10, 12, 14 and 16, as their tendency to equality is sufficiently obvious.

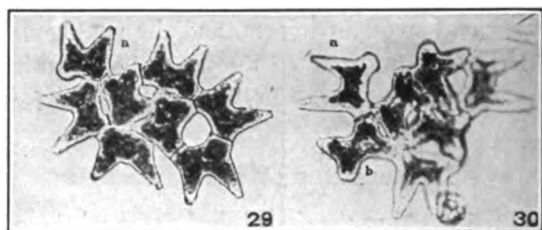
The corresponding radial walls between the cells of series II. tend to be equal as do also the radial walls between the cells of series III. The indication from the measurements of the selected colony that the walls i and i^6 of the central cell should be regarded as typically a little longer than the walls i^1 and i^5 is not confirmed by the measurement of the series, though there is a difference of .2 mm. in the average. Measurements of the dimensions of the central cell in a larger series of colonies would be of interest. Its inherited oblong and two-lobed form, and the pentagonal outline in the colony formed by the bases of the five cells of series II. afford an interesting case of disharmony in morphogenetic factors.

INHERITANCE OF CELL FORM.

I have pointed out that the four-lobed form of the cells appears immediately in the young colonies and have referred to it throughout as inherited rather than as the direct and epigenetic expression of the pressure and other interrelations of the cells in the growing colony. I have pointed out the adaptation of this four-lobed cell form to the exigencies of group formation, when the number of units is strictly limited by the principle of bipartition. The principle of least surfaces here requires that five cells instead of six are to be placed about one in the center and ten cells in the third series. This arrangement involves just such a tangential elongation of the individual cells as we find has actually occurred and favors the maximum of compactness in the arrangement $1 + 5 + 10$. I have suggested the possibility that the environmental complex may have led in successive generations to the development of this four-lobed form and its fixation as an hereditary character of the cells. Evidence that the typical form of the cells can be achieved independently of their being in normal contact and pressure reactions in the colony is rather easy to obtain. Many colonies are found in nature

in which by some accident certain cells are only attached at one point to the remainder of the group.

In Fig. 29 we have an eight-celled colony of *P. asperum* in which one cell, *a*, is attached by only one of its basal lobes and yet is quite symmetrically developed. The second base lobe is rounded rather than sharply wedge-shaped and this difference may be taken as the measure of the influence of the epigenetic pressure and contact relations as compared with heredity in determining the form of the cell. The asymmetric positions of the two central cells in this colony also have produced characteristic effects on their form and it is plain that the relatively free cell has much more nearly achieved its full development than have these

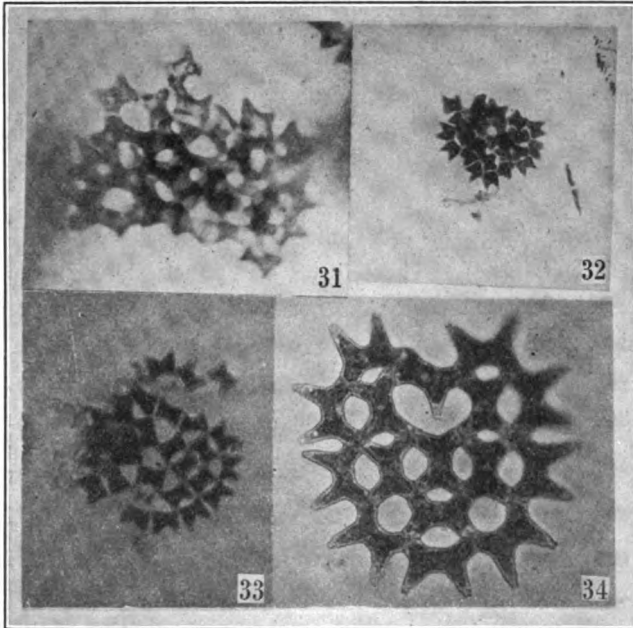


FIGS. 29 AND 30. *P. asperum*. Irregular, eight-celled colonies, one cell in each case attached by one lobe only, but quite typical in outline. \times about 550.

cells with their asymmetric contact relations. In Fig. 30 we have a colony with only seven cells visible, one cell, *a*, attached by only one basal lobe, another by a basal and a peripheral lobe, *b*. It is plain here that in neither case has the free basal lobe tended in any degree to assume the more tapering form of a peripheral lobe, nor have the long and short axes of the cells been reversed. In this colony the eighth cell may have been present in its early life and possibly may have been connected with some of the cells now partly free. The form of cell *b*, however, has certainly been achieved under the same contact conditions in which it appears in the figure. The rounded end of its free basal lobe as well as that of cell *a* shows that the wedge form is an environmental effect.

Figs. 31 and 32 (less highly magnified) also show cells which have attained the normal form while attached by only one basal

lobe. These are probably thirty-two-celled colonies, though they are too irregular to permit accurate counting. The colony shown in Fig. 31 is quite young, while that shown in Fig. 32 is well on toward maturity. The cells attached by only one lobe have gone through their whole development in apparently normal fashion.



FIGS. 31 AND 32. *Pediastrum asperum*. Young colony showing as in Figs. 29 and 30 cells which are without their normal contact and pressure relations in the colony and have still developed the characteristic form for the species. Fig. 31 \times about 500; Fig. 32 \times about 175.

FIG. 33. *P. asperum*. Like the last two figures, but with a cell attached in reversed position by one of its peripheral lobes and still showing the typical form. \times about 225.

FIG. 34. *P. asperum*. Colony with one of its peripheral cells reversed but showing one typical long spine directed toward the center of the colony. The other is blunted by contact with an adjacent cell. \times about 425.

Most interesting is the case shown in Fig. 29, where we have a cell attached only by one of its peripheral lobes and to a peripheral lobe of a peripheral cell of the colony. Here the basal lobes are both peripherally placed and yet have retained their blunter form.

The peripheral lobes are basally placed and one of them functions for attachment and yet they retain their more tapering form. .

It is over and over illustrated in abnormal colonies that the polarity shown in the difference between the basal and peripheral lobes is a matter of cell organization and not of colony organization. A very characteristic case is shown in Fig. 34. Here in an otherwise quite regular colony one of the ten peripheral cells has been reversed in position and thrust partly back into the second series. The one free peripheral lobe is quite normally developed though pointing toward the central cell of the colony. The diagonally opposite basal lobe which is free to grow radially outward has shown no tendency to do so. The second true peripheral lobe has had its natural growth tendencies quite inhibited by the limitations of space in which it finds itself. The tendency to functional hypertrophy if operative here is not equal to the production of a normal peripheral lobe under such conditions. The whole grouping in such a case gives a very clear picture of the exact part played by heredity and environment respectively in morphogenetic processes.

Such examples as are shown in Figs. 25-30 can be multiplied almost without limit and it is clear that however much the contact and pressure relations in the group may have influenced the evolutionary processes by which such oval cells as those of *Gonium* become the four-lobed oblong cells of *Pediastrum*, at present these cells are able to attain their characteristic forms, diagnostic for the species, when almost entirely free from their normal environmental relations with the other cells of the colony.

Nitardy figures several marked cases ('14, Taf. VI., p. 2) in which the single spinous outgrowth and general triangular form of the cells of *P. simplex* are shown to be an hereditary growth-habit of the cells rather than a response to their pressure relations of orientation in the colony. In the figure referred to a peripheral cell is shown with its poles reversed and the spine projecting toward the center of the colony and an intercellular space quite as in my Fig. 30 described above.

It would be natural, perhaps, to expect that the four-lobed form should be strictly epigenetic and achieved anew by each generation

under the influence of the stresses and pressures developed in the growing colony. We have noted, however, that the cell form characteristic for the species is visible at once as the swarmspores cease moving and is only sharpened and made more definite with the further growth of the cells. On the other hand, it is equally obvious

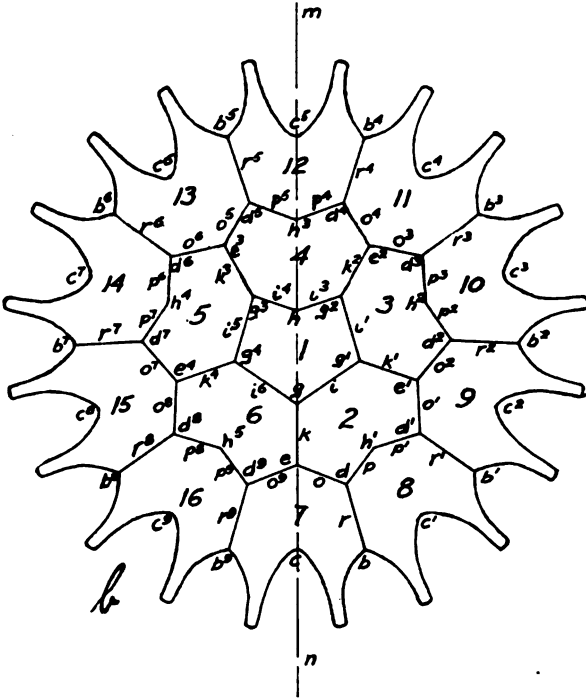


FIG. 35. Type diagram from a selected individual, colony No. 55. Reproduced from '16, Fig. 1b.

that abnormalities of form—shortening, elongation, change of direction of the lobes, etc.—as well as the regular blunting of the peripheral lobes of interiorly placed cells are all direct environmental epigenetic results dependent on the interrelations of contact and pressure between the cells in the forming and growing stages of the colony.

GENERAL DISCUSSION.

Cell Form.—There are plainly two sets of form-determining influences operating on the cells of *Pediastrum*. First, the cell heredity which, given free play, as in the case of cells largely out of contact with other cells of the colony, develops what we may call the typical cell form. And, second, the environmental pressure and contact relations which exist between the cells as ordinarily placed in the colony. This may result in the extreme difference which we find between the internal and peripheral cells of *P. Boryanum* or the very slight differences which we find between these same cells in *P. clathratum* (Fig. 3). The familiar antithesis between heredity and environment in the determination of adult form and structure is fully in evidence in *Pediastrum*, but under such relatively simple conditions as to permit of an attempt at analysis. It is obvious here, as has been held in general by students of heredity, that inheritance through cell division may perpetuate the type form and structure, while many at least of the fluctuating variations in the type are directly traceable to environmental conditions of interaction between the cells and favorable or unfavorable outside conditions at the time the colony is formed and during its growth.

The evidence is clear, as I have shown from the cases of accidentally misplaced cells, that all the various cell forms found in the genus are transmitted from one colony to the next by inheritance in some fashion or other. I shall discuss the method of transmission below. The cell form also obviously determines the character of the colony as a whole. The form and character of the colony as a whole may be said also in turn to influence the form of the cells, but the modifications so produced are of the nature of environmental limitations on the complete development of the cells, as, for example, the shortening of the lobes on the interior cells as compared with the marginal cells of the colony. The position of the cell in the colony influences its form only in minor, though perfectly obvious and definite degrees, but the structural and organic characters of the colonies which are the basis for their classification into subgenera and species are the direct expression of the inherited characters of the cells.

The prevailing oblong, four-lobed form of the *Pediastrum* cell is probably adaptive for the general metabolism of the cells and is also the form which permits the closest possible approximation to a least-surface configuration in a colony composed of units arising by binary fission. It is the form of cell which would be expected to arise under the pressure relations existing in such plates of cells held together by adhesion and yet as noted it can and does arise in cells almost entirely free from such contact and pressure relations. We have here evidence that a cell form which may well have arisen first simply as a response to environmental stimuli has become fixed in heredity until now the series of growth processes by which it develops can go on quite independently of the stimulative conditions which originally called them forth. In *Pediastrum* we do not have the extreme differentiation of germ plasm and soma which under the conditions in the higher metaphytes makes such direct interrelations of environment and heredity so difficult to conceive.

It is sufficiently obvious that the oblong four-lobed form is directly transmitted through vegetative reproduction by cell division and there is no reason to question that the same is true in sexual reproduction by the fusion of gametes. In asexual reproduction the mother cell divides by successive bipartitions to produce a swarm of oval ciliated swarmspores which at first show no trace of their adult form. I have noted, however, how promptly, almost instantaneously, the four-lobed form appears as the swarmers come to rest in the contact and pressure relations of the colony and with the very first growth expansion, so that almost as soon as it is formed the young colony has all the essential structural characteristics of the adult.

We may consider briefly at this point the difficult question as to the method of representation and transmission in heredity of the characters of differentiated tissue cells and the characters of tissues, organs and entire organisms considered as wholes.

Inheritance of Cell Form.—The inheritance of cell form cannot be said to be direct in the sense that the inheritance of green color may be direct. The division of a green cell gives at once two green cells. Greenness is inherited as such by division of the chloroplast

and is a metidentical character in Detto's sense. The color as such may be thought of, at least, as present throughout the whole process of producing the daughter cells from the mother cell. The cylindrical form of a cell of *Spirogyra* may also be inherited directly as such in this same fashion by the division of a cylindrical mother cell into two shorter cylindrical daughter cells.

In the case of the cell of *Pediastrum* the lobed or spinous form disappears in the successive bipartitions of the mother cell and we have an oval ciliated swarmspore essentially similar in form to those of other more or less distantly related green algæ. Reproduction by cell division here has involved the return to what is generally assumed to be a more primitive type of cell both as to its form and its motility. The adult form typical of the species only reappears as a result of ontogenetic development by which the primitive cell form becomes differentiated into the more specialized adult. In all filamentous and cœnobic algæ which reproduce by swarmspores we have this advance beyond the conditions in *Spirogyra*, and related types in which the germ cell differs only in size from the adult. The reproductive cycle in *Pediastrum*, for example, parallels that of the higher plants in its essential stages. A mother cell forms undifferentiated germ cells which become specialized during ontogeny in their form and structure and by their combination produce the many-celled colony which shows also a more or less highly specialized and adaptive organization. In the higher metaphytes it is not so directly obvious as in *Pediastrum* that the form characteristics of the many-celled plant body are the direct expression of the form, polarities, adhesiveness, and other characteristics of the individual cells. The inheritance of cell form and of the form of the colony are indirect as compared with cell color. To be sure, in the latter case swarmspores may be relatively or entirely free from the green color which then reappears in ontogeny but the transfer of the capacity to form green pigment is assumed to involve the division of plastids which thus carry on the pigment-forming bases, chromogens, just as the nucleus, chromosomes, etc., are perpetuated directly by division. In the vegetative reproduction of these simple algæ we do not need to say that the capacity to form chlorophyll is represented by an hereditary factor in the germ plasm,

for we have the visible organ or plastid of the cytoplasm to provide for such transfer. The evidence as to the behavior of the plastids in zygospore formation in *Spirogyra* indicates that the same is true in sexual reproduction by cell fusion. In the case of the lobed cell form, however, every visible trace of the adult character as such seems to be lacking in the germ cell, and it seems natural to postulate a gene or factor which without being the character itself may as a granule or in some other form represent the adult form when it has disappeared. As a matter of fact, however, we have no plastid for form determination and to assume a granule like a plastid in the chromosome which transmits the determiners of the adult cell form meets with obvious difficulties in this case. The sudden appearance of the lobed, spinous cell form in reproduction as I have described it does not suggest the working out of influences emanating from elements in the chromosomal organization of the nucleus, but rather the direct expression of the organization of the cell as a whole when it begins to grow. This organization shows the most direct relations of adaptation to and interdependence with the pressures and contacts established in such a group of cells and may well have been achieved as a response to such environmental surroundings, but it is quite independent of them and comes to full expression, as noted, in cells which are for accidental reasons quite free from the other members of the colony. It seems to me to be most obviously the expression of the anomogenous organization of the protoplasmic mass involving localized growing points on its surface, specific polar differentiations, etc. This general organization of the cell may well be transmitted indirectly through cell division involving as such transmission would only a sort of regeneration by each daughter cell of the general symmetry relations between the parts of the mother cell.

We do not need, then, as it seems to me, to imagine any spatially differentiated organization of a special germ plasm to account for the inheritance of cell form in *Pediastrum*. It would be possible, but probably premature, to attempt to express in diagrammatic form for *Pediastrum* the organization of the cell as a whole which is implied in its behavior in forming the colonies. Much further cytological work such as has been done by Smith on nuclear and cell di-

vision, the centrosome, blepharoplast, plastids, pyrenoids, etc., of *Tetrademus* ('13), *Scenedesmus* ('14), *Characium* ('16), *Pediastrum* ('16), etc., is needed before we shall be able to correlate the evidence for cell polarities, adhesions, growing points, surface tension, etc., with the data from the chemical study of colloids. But it is obvious that it is only on the basis of such studies that we can hope to lay the foundations for a proper theory of the hereditary transmission of characters and the morphogenetic processes by which a mother cell is transformed into a mass of free-swimming swarm-spores and these in turn into the adult colony of *Pediastrum*.

Inheritance of the Characters of the Colony.—The characters of the colony as a whole, however, may seem to involve a much more indirect and hence perhaps properly a factorial representation in the germ cell, but such a conclusion seems to me quite unwarranted. I have elsewhere in a number of cases emphasized the incommensurability of the organization of the cell and that of the many-celled body. Driesch ('05) has shown the impossibility of a preformation which demands even the simplest possible three-dimensional representation of the organization of the adult in the organization of the germ plasm.

The characters of the colony as a whole are dependent, as noted, directly on the form, polarities, adhesiveness, surface tension, etc., of the individual cells. These are characters of the cells as wholes, as protoplasmic aggregates, and there is no reason for conceiving them as especially represented in localized regions of the chromosomes, at least in the case of these simple plants.

We cannot compare cell characters of form with colony characters of form except in the case of some of the simplest surface-tension relations. The colony is an aggregate of cells whose organization is an expression of their cellular interactions in ontogeny. The form characters of the colony may be transmitted down to the details of cell arrangement, shape of intercellular spaces, etc., but these details cannot be conceived as in any way directly represented in a germ plasm.

The complexity of the adult colony is the expression of the differentiation made possible by the interaction of individual cells and their specialization along different lines. An example is found in

the difference between the marginal and interior cells of *P. Boryanum*. The cells all have the same inherited growth tendencies, the differences between them are due to their respective positions in the colony. Such differences are the expression merely of a certain degree of susceptibility to contact and pressure stimuli which, for example, we can think of as greater in *P. Boryanum* than in *P. asperum*. It is certainly more natural to think of such degrees of sensitiveness as characters dependent on the growth reactions of cells as wholes rather than on the presence or absence of a particular chromosomal granule or region.

The organization of the leaf of *Elodea* with its spinous marginal projections affords an interesting parallel in the higher plants. It would be difficult for anyone to conceive that any cell of the leaf might not form a typical spinous projection if it were properly placed on the margin instead of in the interior of the leaf.

We can distinguish then in such cases as those of *Pediastrum* three grades or degrees of directness with which the hereditary transmission of characters is accomplished. First, direct transmission by division, associated with the division of the germ cell, of the particular structural element whose possession constitutes the character, as for example the transmission of green color by chloroplasts. Such a character is metidentical, that is, it is the same thing in the germ cell as in the many-celled organism as a whole. Second, the more indirect transmission of the characters of the differentiated adult cells, which are not visibly present as such in the germ cell. Examples are the lobed form of the adult cells of *Pediastrum*. In this case the conceptions here involved can be easily extended to the higher plants. The stellate pith cells of the bulrush and the elongated thick-walled cells of wood and bast can be thought of as in the same category as to heredity and ontogeny as the lobed cells of *Pediastrum*. Such characters express what we recognize as the organization of the cell as a whole including cytoplasm and nucleus, and are hardly to be conceived as represented in any particular part or organ of the cell. Third, the entirely indirect transmission of the characters of the many-celled organism as a whole, in *Pediastrum*, such characters as the plate-shaped form of the colony, the presence or absence of perforations, the arrangement of the cells,

and the degree of difference between the interior and peripheral cells. It is obvious in *Pediastrum* that such characters are determined directly by the characters of the cells, but it is equally clear that except in their simplest features they are incommensurable with those of the individual cells and cannot be represented directly as such in the germ cell. It is the form, adhesiveness, polarities, etc., of the cells that determine the character of the colony and these characteristics of the cells as noted can best be conceived as characters of the cells as wholes rather than as determined by particular unit parts of cell organs or even by entire cell organs. The general growth tendencies of the cell are characters of the cell not of the colony as a whole and can come to expression regardless of whether the colony is formed or not.

Evidence of Polarity in the Cells.—Furthermore it is obvious as shown above that each cell has a specific orientation in the typical colony, and yet there is no mosaic heredity. Any one cell can replace any other cell in the colony and the shape of the cell is in many species in no notable degree a function of its position or interrelations with the other cells. Each cell in the typical arrangement has its major axis in a definite relation to the major axis of the colony. The long pair of lobes or spines point in general radially outward from the center. This, as I have shown, is not at all because, as one might suspect at first glance, the cell tends to grow its longer spines on whichever side happens to be turned outward. The irregular colonies demonstrate this over and over (Figs 26-28). If in the swarming period the cell does not achieve its normal position with its short axis placed radially and the spine-bearing side outward the maladjustment is never overcome. The long spines push out from the side predestined to produce them and develop as fully as they can under the pressure relations in which they are placed. There is surprisingly little evidence of adaptability in the cells in this regard. Apparently the cell axes are already fixed unalterably in the swarmspore stage and are quite independent of any contact relations then or later established. The presence of a polar differentiation of the axes of the cells in addition to the operation of the principles of binary fission, surface tension, adhesion, functional hypertrophy, etc., is certainly essential in the morphogenetic proc-

cesses by which the plate-shaped colony of one cell layer in thickness and with the longer spines of the cell directed radially outward is formed.

We are confronted here as in practically all higher plant cells with polar differentiation in the cells themselves. The question as to whether this polarity is developed, as is true in so many cases, under the influence of light or gravitation acting during development would seem to be answered in the negative for *Pediastrum*. So far as my observations go, the young colonies are formed in the mother cells at all angles to the direction of the light falling on them and in their orientation to gravitational stimuli. In those cases of rather weak swarming which I have described as forming the oblong instead of circular colonies the shape of the mother cell undoubtedly exerts an influence on the form of the colony. But there is no evidence that the flattened form of the mother cell prevents the swarmspores from making a group of two layers in thickness or an oval mass. The observation of the swarming masses as I have described them suggests most forcibly that, as noted above, the cells actively seek out a position in which they are in equal pressure and contact relations with the adjacent cells right and left of them and with the side which is to develop the large spines or spine radially outward and not vertically upward or downward, involving again in the case of the interior cells contacts with a cell or cells on their basal and peripheral surfaces. No other hypothesis than that of at least a biaxial polarity in the internal organization of the swarmspores seems adequate to account for this definite orientation of the cells in the colony. The existence of the cell axis radial to the colony as a whole is of course most conspicuous owing to the difference in development of the peripheral and basal lobes, but the assumption of a polar differentiation in the tangential axis is equally necessary. The existence of physical polarities or polar differentiations in such complex organisms as the swarmspores with their nuclei, plastids, cilia, etc., is, of course, to be expected. A purely physical factor which may have had phylogenetic significance in the development and fixation of radial polarity is present in the differing lateral pressures to which the basal and peripheral regions of the cells in such a plate-shaped group are subjected. Such differences

in pressure would naturally give a slightly wedge-shaped form to the cells. That this factor is not necessary for the development of the wedge shape of the cell in the formation of the colony now is shown, as I have indicated above, by the fact that the cells will develop their characteristic forms when practically free from contact or pressure relations. The basal and peripheral axial differentiation seems to appear spontaneously now as an expression of the internal organization of the cell whatever may have been its origin, but a slight progressive difference in density from the basal to the peripheral region of the cell may still be one physical condition for such a polarity.

The plate-shaped form of the colony as a whole with one layer of cells plainly depends for its achievement on the transverse or right and left contact relations between of the cells. The cells are so constituted that they achieve contacts with as nearly as possible equal pressures on their right and left sides and, furthermore, so placed that the one or two lobes or spines lie in the plane of these contacts and hence in the plane of the colony as a whole. Such relations can be represented as transverse polarity by the plus and minus or positive and negative analogy, as I have indicated in the colony shown in figure 5. This schematism breaks down in the case of the central cell and for the radial relations of the cells. It is of course only a purely formal representation of the right- and left-sidedness in the cells. There is no visible evidence in the cell itself for the assumption of any structural right and left differentiation. I have found no proof that any particular cell would not find its polarities equally met when rotated through 180° on its radial axis. The only conspicuous evidence of the location of a transverse or tangential axis is in the fact that the spines regularly lie in the plane of the colony.

The assumption of an axis of polarity vertical to the plane of the colony would seem to meet the requirements of the case equally well. The poles would be such in this case as to prevent the cell coming to rest when they were in contact with other cells. However these polar differentiations are conceived it is obvious that some such conditions are necessary for the achievement by free-swimming swarm-spores of a plate-shaped colony of a single layer of cells. That

such morphogenetic factors are organic characteristics of the individual cell rather than the expression of any mysterious form, determining principle residing in the organism as a whole is sufficiently clear, as it seems to me, from the fact that the cell can develop its specific form in entire independence of its interrelations with the other cells of the colony. If, as I think is necessary, one must assume that the cells are characterized by these definite polar differentiations, it becomes still more obvious that the swarming period in its later stages at least when the cells writhe and glide and turn upon each other is not one of aimless movement hither and thither with a final chance distribution of the cells but a definitely directed effort to achieve for each cell a specific relation to its fellows. If the swarmers already had the four-lobed biaxial form we could regard this as a mere matter of physical adjustment analogous to the putting together of the parts of a Chinese puzzle, but as I have pointed out and as earlier students have observed, the cells get their position in the colony as mere oval or egg-shaped jelly droplets. The four-lobed biaxial form appears instantly with the beginning of growth but not before growth begins nor before the cells have their fixed position in the group. It would be highly interesting to know how the cilium-bearing tip, the so-called mouthpiece, of the swarmspore is placed at the moment when the cells come to rest, but I have been unable to determine this point.

It seems to me evident, then, from the shape of the cells and their orientation in the normal colony that they must be regarded as at least biaxial in their relations to each other, the polar differentiations corresponding with their major axes. They are not in equilibrium in their interrelations till the opposite right and left and basal and peripheral poles of their axes are in a general way juxtaposed. In the sixteen-celled colony of *P. asperum* and *P. Boryanum* this would hold for all the cells except the central cell, whose polar relations with the surrounding cells are not easy to analyze. It is perhaps for this reason that the center of the colony is left vacant in the sixteen-celled colonies of *P. clathratum* and the ring-shaped eight-celled colonies of *P. simplex*. The tendency to irregularity in the arrangement of the interior cells of the sixteen-celled colonies of *P. simplex* may also be related to this same difficulty in the polar relations of a central cell in such a group.

Relations of Heredity and Environment to Morphogenesis.—The organization of the colony is determined by the number of the cells resulting always from bipartition, their viscosity, surface tension, mutual attraction and adhesion, their inherited form, whether with one or more spines, and their mutually differentiated polarities by virtue of which they can achieve a definitely oriented relation to each other and thus to the group as a whole. We have here an exhibition of cell qualities influencing morphogenetic processes in such a fashion as to produce a very definite and probably adaptive structural result without any adequate evidence that the characters of the colony as a whole are directly represented in any way in the cells. The form of the colony is achieved in ontogeny as a result of the interactions of the cells.

The characters of the cells are of two classes. First, metidentical as illustrated in the green color, which is transmitted directly by the division of the plastids in which the pigment is borne and, second, characters depending on the organization of the cell as a whole, such as its form, due to its anomogenous consistency from the standpoint of surface tension, its polarities, viscosity, adhesiveness, etc. These cell characters are transmitted in heredity and can be achieved independently of the position of the cell in the colony or any interrelations with other cells. The internal environment of the cell in the colony may modify its form more or less according to the species but is not necessary for its typical development. The close approximation to their normal shape achieved by cells in such irregular colonies as those shown in figures 26, 27, and 28 and in the malformed young colonies (Figs. 21-24) is striking evidence of the fixity of the form characters of the cells as contrasted with the form characters of the colony as a whole. The two types of characters are in different categories.

The influence of the external environment on the form characters of the colony as a whole is most strikingly shown in the differences between colonies in which the swarming has been long continued and vigorous and those in which it has been reduced or has disappeared entirely. There can be no question that in general the colonies of *Pediastrum* are typical in form in direct proportion to the vigor displayed by the swarmspores at the time the colony is or-

ganized. The direct effect of the mother cell vesicle in flattening one or both edges of the plate (Figs. 18-24) in case of slightly weakened colonies is typical of the effect of an unfavorable environment in limiting or inhibiting normal development.

The relative perfection of arrangement of the peripheral and interior cells is also most suggestive of the indirect effects environmental conditions may produce. Statistical studies of the degree of approximation of different colonies to the typical expressed in terms of divergence of cell axes from the axes of the colony as a whole, degrees of distortion of cell form, variation of the angles of intersection of cell walls from 120° , etc., may be expected to afford a reliable index of the effect of environment on the metabolism and growth of the cells.

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DESCRIPTION OF PLATES.

The photomicrographs were made for the most part with the Zeiss apochromatic objective 8 mm. and the compens. oculars, Nos. 8 and 12. They are all of *Pediastrum asperum*.

PLATE V.

FIG. 8. Fairly mature, sixteen-celled colony about ready to form swarm-spores. \times about 225.

FIG. 9. A few cells of a still more mature colony more highly magnified, showing the marked reduction in the size of the intercellular spaces. \times about 1,125.

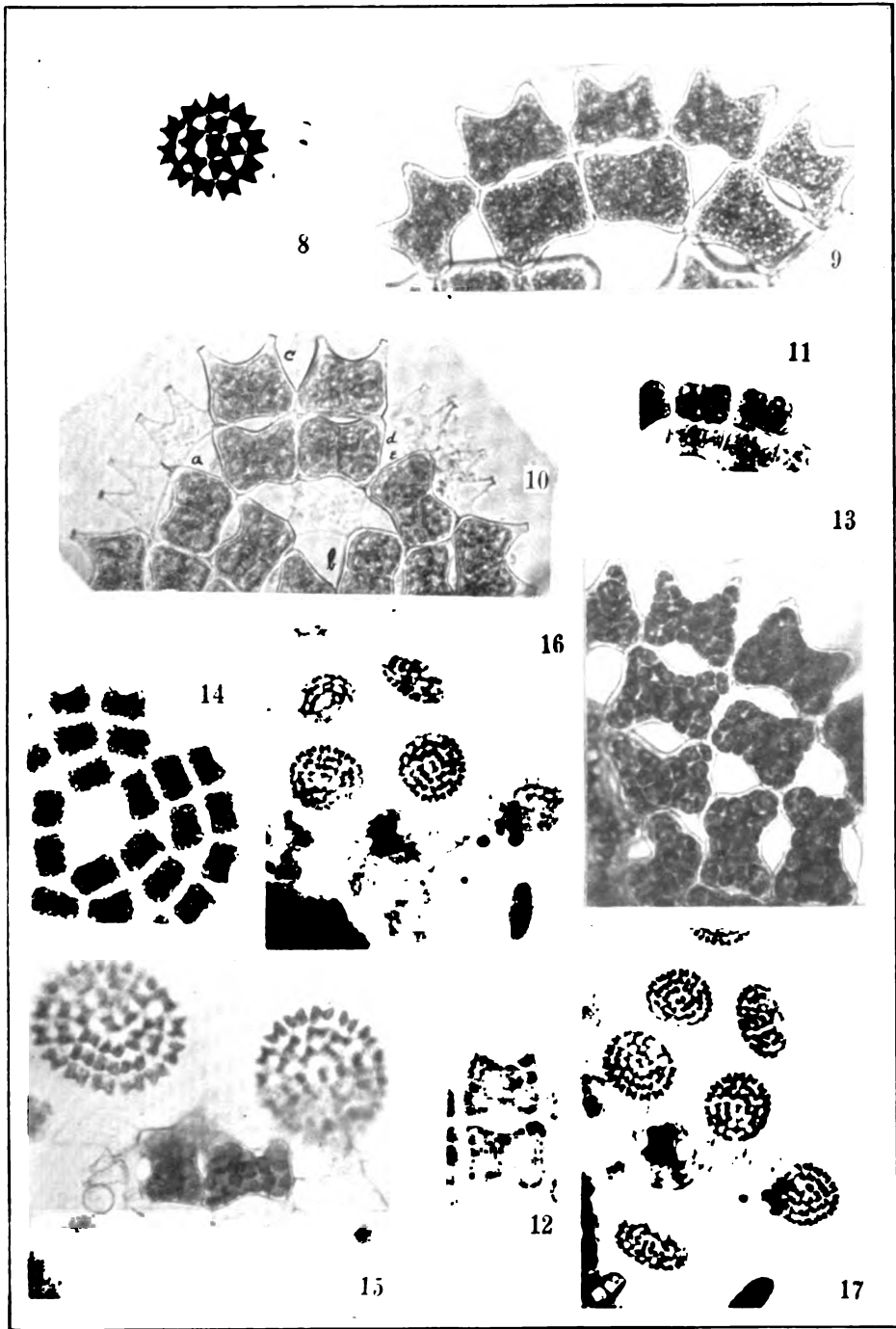
FIG. 10. Cells *a* and *b*, showing two cell stages, the first cleavage in the short axis of the mother cell. Cells *c*, *d* show at least the beginnings of the four cell stages, the second cleavage plane being in the long axis of the mother cell. In cell *e* the planes are more irregular. \times about 1,125.

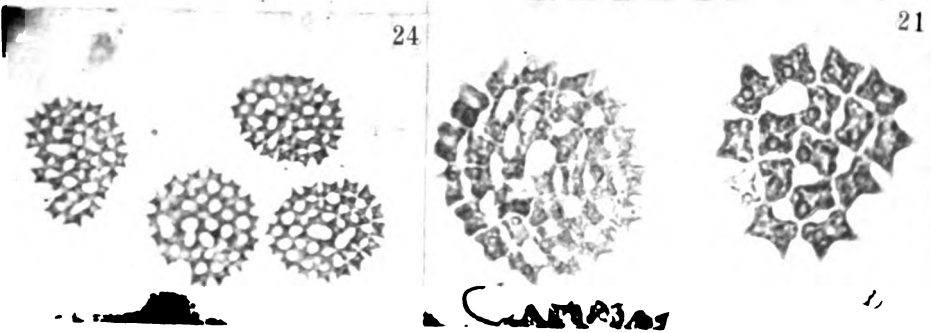
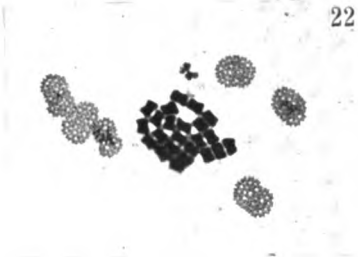
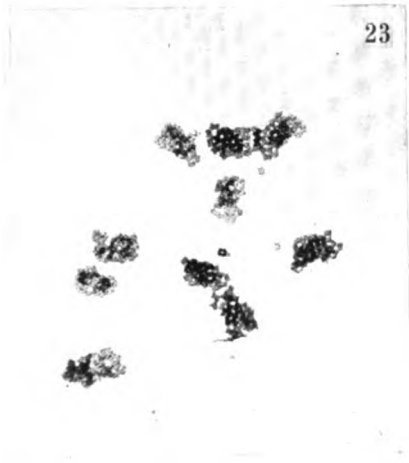
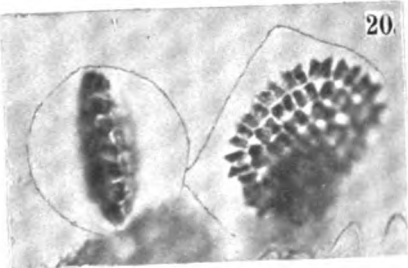
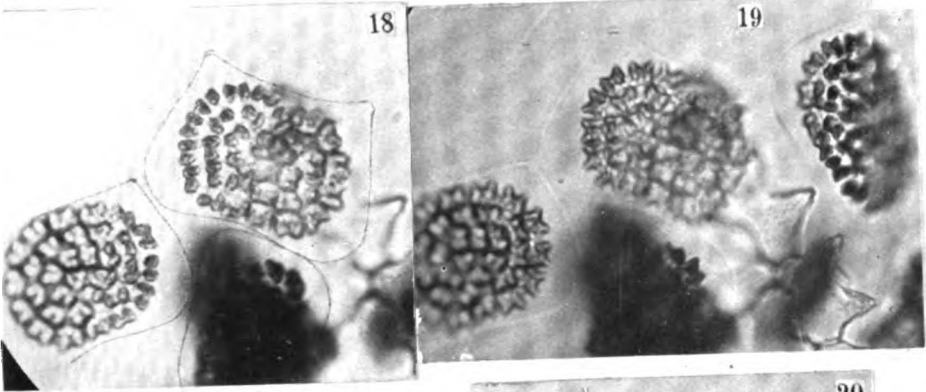
FIG. 11. Eight-cell stage, perhaps later, the planes of cleavage still showing a marked tendency to intersect at right angles. \times about 550.

FIGS. 12 AND 13. Cleavage complete and the daughter cells more or less rounded up. The whole mass conforms to the outlines of the four-lobed mother cell and there is little evidence of the rectangular intersection of the cleavage planes. Fig. 12 \times about 700; Fig. 13 \times about 1,125.

FIG. 14. Less highly magnified view of a thirty-two-celled colony in all of whose cells cleavage is complete. \times about 500.

FIG. 15. Two young thirty-two-celled daughter colonies and two cells





of the same mother colony just ready to swarm. Empty cells of the same mother colony are also shown. The cells of the two daughter colonies already four-lobed and looking almost as if they were dividing in their short axes. \times about 1,050.

FIG. 16. The same group a few minutes later less highly magnified and showing seven daughter colonies and part of an eighth all more or less out of focus. The swarmspores have just escaped from the right-hand mother cell of the two shown in Fig. 15 and appear as a rounded cloud partly beneath the left-hand mother cell. They are swarming vigorously and are also a little out of focus. \times about 500.

FIG. 17. The same group a few minutes later than the stage shown in Fig. 16. The swarmspores have come to rest in the newly formed colony and the rounded outline of the colony and its concentric series of cells can be made out though it is somewhat out of focus in this figure also. \times about 500.

PLATE VI.

FIGS 18, 19 AND 20. Young daughter colonies still enclosed in the vesicles in which they escape from the mother cell. The vesicles are very transparent and hard to bring out in the photographs. In Figs. 18 and 20 I have traced their outlines over with dilute India ink; in Fig. 19 they are left as they appeared in the print and while they are very faint they can be seen and it is clear that in shape they still maintain the outlines of the mother cell even to the slight projections representing the larger pair of spines. The walls of the mother cells, also shown, enable us to compare the size of mother cell, vesicle and young colony. The tendency of the young colony to conform more or less to the oblong shape of the vesicle is obvious, but the edge view of a colony in Fig. 20 shows that in these cases at least this tendency has not prevented the formation of the plate of a single layer of cells though the space relations in the vesicle would favor the formation of two or three layered groups such as are shown in Fig. 23. \times about 1,050.

FIG. 21. Two young daughter colonies, one with sixteen, the other with thirty-two cells, both being the offspring of a thirty-two-celled mother colony. The young colonies are of the same age, but the cells of the sixteen-celled colony are proportionally larger. \times about 500.

FIG. 22. A mother colony and six young daughter colonies, all of which show more or less the influence of the oblong mother cell vesicle on their shape. \times about 150.

FIG. 23. Ten extremely young daughter colonies, all from the same mother colony. Reproduction occurred in this case after the mother colony had been sealed up as described for about eighteen hours and the free swimming movements of the swarmspores were almost entirely suppressed. The colonies are two or more layers thick and the interrelations of the cells are entirely abnormal and yet the cells themselves have taken on the four-lobed form typical of the species. \times about 150.

FIG. 24. Four young colonies from the same mother colony, illustrating still further, as do the preceding figures 15 to 23, the extreme range of fluctuating variation in cell arrangement which can be found in the offspring of a single mother colony, while in all the type of cell form remains quite constant. \times about 400.

LIGHTING IN ITS RELATION TO THE EYE.

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(Read April 13, 1917.)

I. INTRODUCTION.

The work of which this paper is a brief outline was done under the auspices of the American Medical Association's subcommittee on the hygiene of the eye, of which Dr. William Cambell Posey, of Philadelphia, is chairman, and has been in progress for six years. The object of the work has been to compare the effect of different lighting conditions on the eye, and to find the factors in a lighting situation which cause the eye to lose in efficiency and to experience discomfort. In all 52 different lighting situations have been investigated, selected with special reference to the problem in hand. Also a number of miscellaneous experiments have been conducted pertaining to the hygienic employment of the eye.

Confronting the problem of the effect of different lighting conditions on the eye, it is obvious that the first step towards systematic work is to obtain some means of estimating effect. The prominent effects of bad lighting systems are loss of efficiency, temporary and progressive, and eye discomfort. Three classes of effect, however, may be investigated: (1) The effect on the general level or scale of efficiency of the fresh eye; (2) loss of efficiency as the result of a period of work; and (3) the tendency to produce discomfort. A description of tests designed especially for this work has previously appeared in print. Some of these tests have been designed to determine the eye's aggregate loss in functional power, others to aid in the analysis of this effect. Time can be taken here only for the briefest mention of the principles on which they are based. The one with which the greater part of the work has been done is a test for determining the power of the eye to sustain clear seeing. Just two principles are involved in this test. One is that visual acuity or clearness of seeing may be measured by the smallest visual angle

which the eye is able to discriminate; the other, a principle equally old, is that a loss of efficiency in a machine, apparatus, or a living organ or organism will show out more plainly when a prolonged rather than a momentary performance is required. These principles in their simplest terms have been combined into a test of the comparative ability of the eye to maintain its power of clear seeing or aggregate functional activity under different conditions of lighting and under different kinds and conditions of use. Such a test for clear seeing was needed because the conventional acuity test had not been found to be sufficiently sensitive to fatigue conditions to warrant adoption in our work. It, we scarcely need to point out, was designed to test the dioptric condition of the eye and may be used with more or less success as a test of how far a given lighting condition is conducive to clear seeing with a maximum of momentary effort; but it has not the essentials of a fatigue test, nor of its converse, the ease with which clearness of seeing is maintained, which are the features needed primarily for the selection of lighting conditions for the greater part of the work that we are ordinarily called upon to do. Almost, if not quite, as good results, for example, may be gotten with it after work as before when there is every other reason to believe that the eye has suffered considerable depression in functional power. The reason for this is obvious. Although greatly fatigued, the eye can under the spur of the test be whipped up to give almost if not quite as good results as the non-fatigued organ when only a momentary effort is required. If fatigued, however, it can not be expected to maintain this extra effort for a period of time. The demonstration of this fact led early in our work to the introduction of a time element into the test. The principle involved is not a new one. It is merely the application of a very old and well-known one to the work of testing for ocular fatigue. If, for example, a sensitive test is wanted for the detection of fatigue in a muscle, as good results can not be expected if the test requires only a momentary effort on the part of the muscle as would be attained if the endurance of the muscle were taken into account. For our purpose, therefore, the old acuity test subjected to certain features of standardization for the sake of greater reproducibility has been made into an endurance test in which the fatigue or loss of func-

tional efficiency of the eye is measured by its power to sustain clear seeing for a period of time. In operation the test may be described briefly as follows: The power of the eye to sustain a certain standard of acuity for three minutes is measured before and after a 3-hour period of reading from uniform type and paper under the lighting conditions to be tested. That is, by means of a visual acuity test object, with the proper auxiliary apparatus for its control and observation, and a kymograph and chronograph, records are made of the time the eye can be held up to this standard of performance and the time it drops below. The ratio of these quantities to each other, or to the total time for which the record is made, is taken as the measure of the ability of the eye to sustain its power of clear seeing before and after work under the lighting conditions to be tested.

Thus far the analytical tests have been confined to the retina and the extrinsic muscles of the eye. There are four ways in which the retina might be expected to show a depression of functional power: in a lowering of sensitivity to colored and white light; in an increase in the rate of exhaustion to light stimulation and a corresponding decrease in rate of recovery; and in an increase in the lag or time required to give its full response to light stimulation. We have already made tests for the first three of these features for the effect of different lighting conditions and work is under way for the testing of the fourth feature. In the work on the extrinsic muscles we have again found it advisable for the sake of sensitivity in detecting small effects to use an endurance test instead of one requiring only a momentary performance. That is, we have supplemented the conventional abduction and adduction tests by a determination of the power to sustain the coördination of action on the part of these muscles needed for binocular seeing—measured by the power to maintain under strain the accurate combination of binocular images of a simple test-object before and after a period of work under the lighting conditions to be tested. The eyes are put under strain to combine their images to give the needed sensitivity to the test. When this is done even when the muscles are fresh, if the object is looked at or fixated for an interval of time, it will be seen alternately as one or as two. The proportion or ratio of the time seen as one to the time seen as two or to the total time of the observation can

be regulated by the amount of initial strain under which the eyes are put to combine their images. The regulation of this ratio is empirical and of importance; for, as is the case with the test for loss of efficiency for clear seeing, the sensitivity of the test depends to a considerable extent upon the initial value that is given to this ratio. The eyes may be put under strain to combine their images by interposing between them and the object viewed weak prisms and by adjusting them and regulating the distance of the object from the eye so that with the maximum of effort to see it as one, it is seen alternately as one or as two in the proportion desired.

We have also tested the tendency of different conditions of lighting to produce ocular discomfort, and have explored the field of vision for the purpose of determining the liability to discomfort from the exposure of the eye to surface brilliancies of different orders of magnitude. This tendency was measured by the time required for just noticeable discomfort to be set up, in the former case both with the eye at work and at rest under the lighting conditions in question, and in the latter with the eye systematically exposed to a given area and brilliancy of surface at different points in the visual field, by means of a large perimeter constructed especially for the purpose.

The following aspects of lighting sustain an important relation to the eye: the evenness of illumination, the diffuseness of light, the angle at which the light falls on the object viewed, the evenness of surface brightness, the intensity of light, and its composition or color value. For convenience of treatment in this paper we have grouped the first four of these under the heading distribution factors. The work throughout has been conducted primarily for the purpose of finding out the comparative importance of these factors to the comfortable and efficient use of the eye rather than to test the merits of various types and varieties of lighting. On the other hand, however, the investigations have not been abstract in character. That is, all the variations obtained were gotten in actual lighting situations by employing so far as possible lighting installations in common use. In order that a correlation might be had between lighting conditions and effect on the eye, the following specifications of illumination effects and conditions was made in each case.

1. A determination was made of the average illumination of the test room under each of the installations of lighting used, and of the distribution of light in the room. The room was laid out in 3 ft. squares and measurements were made of the horizontal, vertical and 45° components of illumination at 66 of the intersections of the sides of these squares, and at the point of work. In all cases in which the variation of intensity was not the special point of investigation, the illumination for each installation was made as nearly equal as possible at the point of work.

2. A determination was made in candlepower per square inch of the brightness of prominent objects in the room, such as the test surface and reading page; the ceiling spots above the reflectors for the indirect installations; the reflectors and the ceiling spots above the reflectors for the semi-indirect installations; the reflectors, openings of reflectors and the lamps in so far as they were visible for the direct installations; the specular reflections from surfaces, etc.; and the surfaces of lowest brightness to get the range.

3. Since the angle of presentation is an important feature in the effect on the eye, a determination was made also of the angle of elevation of some of the more important surfaces such as the reflector, opening of the reflector, etc., above the plane of the observer's eye when held in the working position.

4. Photographs were taken of the room from three positions under each system of illumination.

In the selection and use of observers for the work the following are some of the precautions that were taken: Care was exercised in the first place to choose only those who had shown already a satisfactory degree of precision in other work in physiological optics and whose clinic record showed no uncorrected defects of consequence. All were under 30 years of age. Before being allowed to take part in the actual work of testing each observer was trained to a satisfactory degree of precision in the 3-minute record under a given lighting condition and in the 3-hour test under several of the conditions to be tested. In the actual work of testing the results were compiled from several observations and the precision was checked up by the size of the mean error. No results were accepted as significant unless the variation produced by changing the conditions to be

tested was largely in excess of the mean variation or mean error for each condition tested. This, the accepted conventional check on the influence of variable extraneous factors was carefully applied at each step in the work.

In attempting to make any presentation of results for a problem so complicated as the one under investigation, in the space allotted, we have had to choose between giving the details for some particular piece of work and trying to draw some general conclusions from the work as a whole, supplemented by an incomplete statement of data,¹ so far as the tests have been applied up to the present time. We have chosen the latter alternative, although caution and our own preference are on the side of the former.

As already stated, the work has been in progress for six years.

¹ For a detailed statement of the data obtained in these experiments the reader is referred to the *Transactions of the Illuminating Engineering Society*, 1913, VIII., pp. 40-60; 1915, X., pp. 407-447; 448-501; 1097-1138; 1916, XI., pp. 1111-1137; 1917, XII., pp. 464-487.

In these references will be found data on the following points for the lighting conditions tested: (a) The horizontal, 45° and vertical components of illumination at the 66 stations in the test room, the mean deviation of these values from the average illumination and the percentage mean deviation in some of the more important cases. (b) Measurements in candlepower per square inch of the brightness of prominent objects in the room, such as the test surface, the reading page, the ceiling spots above the reflectors for the indirect installations; the reflectors and the ceiling spots above the reflectors for the semi-indirect installations; the specular reflections from surfaces; etc.; and the surfaces of lowest brightness to get the range. (c) Ratios between surfaces of the first, second, third, etc., order of brilliancy and surfaces of the lowest order of brilliancy, and between surfaces of the first, second and third order of brilliancy and the brightness at the point of work, to show the gradations in surface brightness. Again in some of the more important cases the mean deviation of the brightness values of the different surfaces from the average brightness of all the surfaces measured, and the percentage mean deviation have been given. (d) The angle of elevation of some of the more important surfaces such as the reflector, opening of the reflector, etc., above the plane of the observer's eye when in the working position. (e) Photographs for each system of illumination representing to the eye the details of the test room, the location and type of lighting units, the position of the test station, the apparatus with which the tests were made, the illumination effects (distribution of light and surface brightness), etc. And (f) tables giving a detailed numerical statement of the results of the test including among other items a comparison of the average error of each set of determinations with the change of result produced by changing the lighting conditions tested, as a check on the significance of the results.

We have avoided, therefore, as far as possible, making any comparison of results in different series or years; but wherever this has been done, the comparisons are based on the results of the same observer with sufficient check experiments to show that the error of observation is safely within the variation in result upon which the conclusion is based. The following are some of the results that have been obtained.

1. Of the lighting factors that influence the welfare of the eye, those we have grouped under the heading distribution are apparently fundamental. Thus far in the work they seem to be the most important we have yet to deal with in our search for the conditions that give us the minimum loss of efficiency and the maximum comfort in seeing. If, for example, the light is well distributed in the field of vision and diffuse and there are no extremes of surface brightness, our tests indicate that the eye, so far as the problem of lighting is concerned, is practically independent of intensity of light. That is, when the proper distribution effects are obtained, intensities high enough to give the maximum discrimination of detail may be employed without causing appreciable fatigue or discomfort to the eye. The work on composition or color value of light is still in progress. While, therefore, we are not in a position to conclude fully on this point, our belief based on the work which has been done is that the color differences that are ordinarily present in artificial light are not nearly so important as are, for example, the differences in the precautions that are being used to exclude high brilliancies from the field of view. The defects with regard to color value are, however, as a practical problem harder to remedy.

2. For the type of control of distribution factors given by the semi-indirect reflectors of low and medium density and the direct reflectors which present, as many of them do, excessive brilliancies due to opening, surface of reflector, or wholly or partially exposed sources, our results show that often too much light is used in ordinary work for the comfort and welfare of the eye. That is, with these reflectors, means have not yet been found to produce this amount of light without introducing harmful brilliancies into the field of view.

3. The angle at which the light falls on the object viewed is an

important factor especially if the light is not well diffused and the surface of the object viewed is not sufficiently mat in character; but not so important, for example, as a certain evenness or gradation of surface brightness in the field of view. High brilliancies in the field of view seem in fact to be the most important cause of the eye's discomfort and loss in power to sustain clear seeing in lighting systems as we have them at the present time. In lighting from exposed sources it is not infrequent to find the brightest surface from one million to two and one half million times as brilliant as the darkest; and from three hundred thousand to six hundred thousand times as brilliant as the reading page. These extremes of brightness are, our tests show, very fatiguing to the eye, especially when the high brilliancies occur in certain zones or regions of the field of view.

4. Of the commercial systems of artificial lighting tested thus far, unmodified, the best results have been obtained for the indirect systems, and the semi-indirect systems with reflectors having a high density. By means of these reflectors the light is well distributed in the field of view and extremes of surface brilliancy are kept within the limits which the eyes are prepared to stand. A great deal of loss in power to sustain clear seeing has been found to result from the use of semi-indirect reflectors of low and medium density and from the use of direct reflectors of shallow and medium depth. With regard to the degree of density that is most favorable to the eye, the direct reflector seems, however, to present a special case. With translucent reflectors of medium depth, our best results have been gotten so far with reflectors of medium density. This, however, is not in contradiction to our principle that extremes of brightness are fatiguing to the eye. For if the physical efficiency of the reflector is not to be lowered by increasing its density, its opening must become brighter in some proportion to the increase of density; i. e., in a totally opaque reflector all, and in the denser reflectors nearly all of the light sent to the working plane must come from the opening. Moreover, in case of the denser reflectors, the ceiling and the reflectors are relatively dark, while standing out in sharp contrast to them is the bright opening of the reflector. In the reflectors of medium density, however, the reflector need not have such a high brilliancy and there is little contrast between it and its surroundings.

When installed on or near the ceiling in rooms of moderate height, the best results seem to be obtained when the opening, the surface of the reflector and the ceiling have as nearly as possible equal brilliancy. It seems probable that the effect on the eye of the denser reflectors can be very much improved by increasing the depth of the reflector and by other devices that will lower the brilliancy of the opening. In fact the best results we have as yet gotten from any type of reflector have been from a direct opaque reflector of the deep bowl type, modified so as greatly to reduce the brightness of the opening, giving a field of view with the lowest maximum of brilliancy of any we have as yet been able to obtain in an actual lighting situation. This reflector, $10\frac{1}{4}$ in. in diameter and $11\frac{1}{2}$ in. deep, was lined to a depth of 3.7 in. with a mat surface having a reflection coefficient of about 4 per cent. Moreover, a result almost as good as any we have obtained by indirect lighting was gotten by giving this band or lining a reflection coefficient of about 38.5 per cent. In the former case the brightness of the opening taken from the position of the observer's eye was 0.0129 cp. per sq. in., a reduction of 99.8 per cent. in the maximum brilliancy of the opening; and in the latter, 0.1815 cp. per sq. in., a reduction of 96 per cent. In the former the illumination of the room was reduced on the average 25 per cent.; and in the latter, 12.4 per cent. Poor results are given by shallow direct reflectors of all densities unless they are installed so high above the working plane as to be almost if not entirely removed from the field of view.

5. We have frequently been asked to fix an upper limit of brightness which the eye can stand without any considerable loss in power to sustain clear seeing through a period of work. At present this can be done at best only very approximately; moreover, the value assigned can not be made independent of the grouping of conditions in which this brightness occurs. For example, a lighting installation which has its highest brightness well within the field of view demands a smaller maximum than one in which these brightnesses are carried outside the zone of most harmful effects on the eye. That is, higher brightnesses can be tolerated for the totally indirect reflectors, or for direct reflectors installed on the ceiling, than for semi-indirect reflectors in case of which the highest brightnesses,

namely, the brightnesses of the reflectors, are in rooms of moderate height dropped well into the field of view. It is obvious also that the effect will depend on the number and size of the bright surfaces in the field of view as well as on the angle of presentation to the eye. For rooms of the size of the one in which we worked, an approximation of a maximum brightness may be gotten from the following data based on the testing of 52 lighting situations. For the indirect installations the eye fell off 8.6 per cent. in power to meet the standard imposed by the test as the result of 3 hours of continuous reading with the maximum brightness in the field of view of 0.138 cp. per sq. in. For the direct installation the loss was 6.6 per cent. for a brightness of 0.0129 cp. per sq. in.; 8 per cent. for a brightness of 0.1815 cp. per sq. in.; and 32.9 per cent. for a brightness of 0.66 cp. per sq. in. For the semi-indirect installations the loss was 15 per cent. from a brightness of 0.264 cp. per sq. in.; 48 per cent. for a brightness of 0.361 cp. per sq. in.; and 60 per cent. for a brightness of 0.614 cp. per sq. in. We would not feel inclined to recommend a maximum brightness greater than 0.15–0.2 cp. per sq. in. with the grouping of distribution factors ordinarily found in the lighting of rooms. In contrast with this, the brightness of the gas flame and oil lamp is from 3–8 cp. per sq. in.; the Welsbach mantle from 20–50 cp. per sq. in.; the carbon filament from 375–480; the filament of the vacuum tungsten lamp from 875–1,000; the filament of the gas-filled tungsten lamp 10,271–16,433; and the open arc lamp from 10,000–50,000.

6. A marked characteristic of the effects produced by the dense and completely opaque direct reflectors was the low illumination of the ceiling and upper part of the room, and the high and in some cases almost glaring illumination of the floor and objects in the working plane. So far as the effects on the eye of the kind registered by our tests are concerned, however, these irregularities of illumination and of low surface brightness extraneous to the lamp and reflector seem to be of comparatively little consequence, so long as the higher brilliancies of lamp and reflector are themselves properly taken care of. With the direct reflectors, translucent and opaque, we have had quite wide variations in the distribution of illumination ranging from the well-illuminated ceilings and the com-

paratively evenly illuminated walls and working plane for the reflectors of medium density to the dark ceilings and upper part of the room and highly illumined lower half for the opaque reflectors. And with the opaque reflectors turned towards the ceiling, the translucent reflectors turned both up and down, and with reflectors of both the focusing and distributing types, we have had the greatest amount of light first in the upper half of the room, then in the lower half, and within limits lanes of light have been produced; still it has been possible to get in all of these cases comparatively good effects on the eye so long as no excessive brilliancies were introduced in the field of view. Again, however, we do not wish to say that this is the only factor that makes for the welfare of the eye. We wish only to call attention to its very great importance.

7. The problem of installing is not the same for the semi-indirect as for the totally indirect reflector. In the latter case the height should be adjusted so as to give as nearly as possible an even distribution of surface brightness on the ceiling and evenness of illumination on the working plane. In the case of the semi-indirect reflectors, especially those of low and medium densities and in rooms of medium height, if the distance from the ceiling is made great enough to produce these effects, the bright reflectors are dropped too low in the field of view for the highest comfort and efficiency of the eye. Apparently the denser they are, the more nearly they should be installed as are the indirect reflectors; and the less dense they are the more nearly they should be installed as are the direct reflectors of similar density, so far as eye effects of the kind revealed by our tests are concerned. In this connection it may be pointed out that in current practice direct reflectors for general illumination are usually installed on the ceiling or as near to it as is possible, especially in rooms of low and medium height. However, while this may be a good general rule for the installation of direct reflectors of low and medium density and of shallow and medium depth, the question of most favorable height for the dense and completely opaque reflectors is, we believe, still open to investigation.

8. In the work of providing general illumination the most difficult feature presented in the problem of protecting the eye is en-

countered in the lighting of rooms of low and medium height. The difficulty decreases with increase of the height of the ceiling. In rooms whose ceilings are very high in proportion to other dimensions of the room, it seems safe to say that comparatively good results could be gotten with almost any reflector of modern design; for it is much easier in such rooms to get the bright sources of light, primary and secondary, out of the zone of most harmful influence on the eye.

9. The loss of efficiency sustained by the eye in an unfavorable lighting situation seems to be muscular, not retinal. The retina has been found to lose little if any more in efficiency under one than under another of the lighting systems employed.

10. The observation of motion pictures for two or more hours causes the eye to lose heavily in efficiency. The loss decreases rather regularly with increase of distance from the projection screen. It seems little if any greater, however, than the loss caused by an equal period of steady reading under much of the artificial lighting now in actual use. In making these tests care was taken to choose a projection apparatus which gave a picture comparatively steady and free from flicker.

11. In all the conditions tested a rather close correlation is found to obtain between the tendency of a given lighting condition to cause loss of visual efficiency and to produce ocular discomfort. The tendency to produce ocular discomfort, as already stated, was estimated by the time required for just noticeable discomfort to be set up with the eye both working and at rest under the conditions to be tested. The results of this work were also carefully checked up by the determination of the mean error of the observation.

II. SOME OF THE CONDITIONS TESTED (COMMERCIAL TYPES OF LIGHTING).

The tests throughout the work were conducted in a room 30.5 ft. long, 22.2 ft. wide and 9.5 ft. high. In Fig. 1 this room is shown drawn to scale: north, south, east and west elevations, and plan of room. In the plan of room are shown by a cross and the appropriate numeral the 66 stations at which the illumination measure-

ments were made; also the positions of the outlets: *A, B, C, D, E, F, G* and *H* for the lighting fixtures. In the drawing east elevation, one of the positions at which the tests were taken is repre-

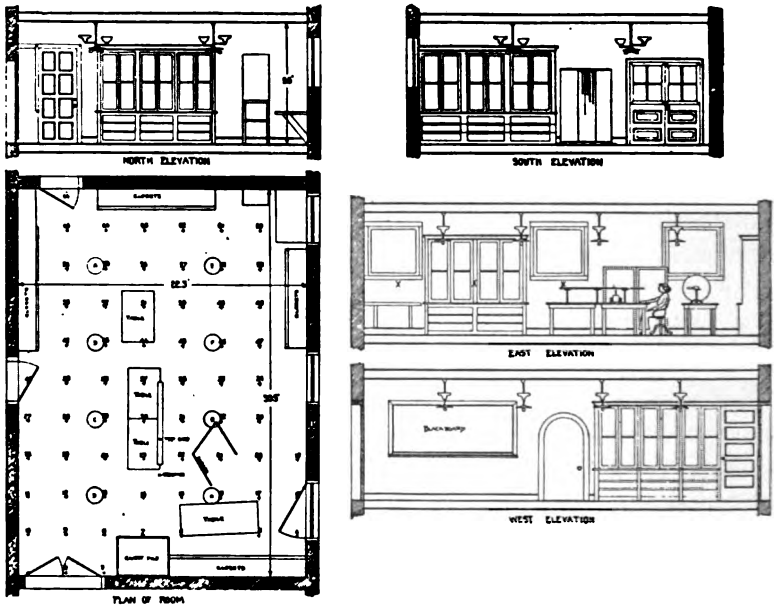


FIG. 1. Plan of test room.

sented, namely, the one with six reflectors in the field of view. The walls and ceilings of this room are of rough plaster painted a mat white. The floor is of medium dark tiling.

1. *Direct, Semi-indirect and Indirect Systems of Lighting.*

In our choice of the first set of conditions to be tested it was our purpose to make a selection that would give a wide variation in the distribution factors. Three types of lighting were chosen. One may be called an indirect system; one a direct system; and one a semi-indirect system. The direct reflectors were not of the most modern make, although they may be said to have given effects very similar to much of the lighting in actual use at the present time. They were of porcelain ware 16 inches in diameter and only slightly

concaved. When placed above the lamps employed, they served merely to direct the light to the working plane. No protection from the brilliancy of the light source was afforded to the eye. For the semi-indirect system inverted alba reflectors 11 inches in diameter

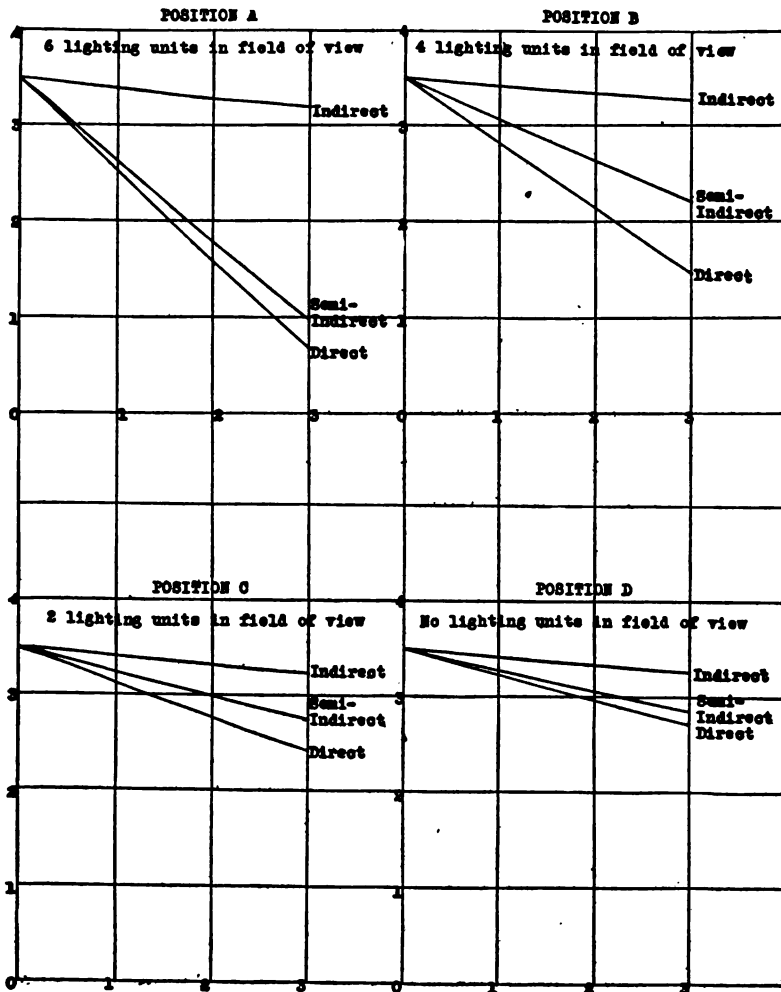


CHART I. (Direct, Semi-indirect and Indirect Systems of Lighting.) Showing the power of the eye to sustain clear seeing under direct, semi-indirect and indirect systems of lighting, and the effect of varying the observer's position in the room or the number of bright sources, primary and secondary, in the field of vision. Power to sustain clear seeing before and after work is represented on the ordinate and hours of work on the abscissa.

were employed. These reflectors are of modern design and represent very well glassware of medium density. In case of the indirect system corrugated mirror reflectors were used inclosed in brass bowls. These reflectors are also of modern design and give effects which may be taken to represent very well those obtained in good indirect lighting. The tests were taken at four positions in the room, one with six, one with four, one with two, and one with none of the lighting units in the field of view. The last three of these positions are marked with a cross in Fig. 1, east elevation. A graphic representation of the results of the tests for the four positions is given in Chart 1. Because of the amount of space that it would require, a tabular statement of results from which these and subsequent charts were constructed will not be given in this paper.

In the second series of experiments we undertook to determine the most favorable intensities of illumination for the three types of installations we had used in the first series; and in addition the effect of varying the intensity of the illumination with the particular grouping of distribution factors represented in each case. The tests were made in the same room, with the same fixtures, and in general with the same conditions of installation and methods of working as were described in the account of the experiments of the first series. To secure the various degrees of intensity of light needed, lamps of different wattages were employed. In order to keep the distribution factors as nearly constant as possible for a given type of system, the lamps used in making the tests for that type of system were all of one wattage, *i. e.*, were all 15's, 25's, 40's, 60's, or 100's. For the indirect and semi-indirect systems 25, 40, 60, and 100-watt lamps were employed. Our fixtures for the direct system were so installed that either one or two lamps could be used in each fixture, totalling respectively 8 and 16. In order to get a wider range of intensities both numbers of lamps were used, *i. e.*, one series of tests was made with 8 lamps, and another with 16. Also four intensities of light were employed in each case. These intensities were secured in the 8-lamp system by using lamps totalling 120, 365, 400 and 800 watts. In case of the semi-indirect and indirect reflectors socket extenders had to be used with the 25 and 40-watt lamps. That is, without the extenders these lamps,

on account of their smaller size, came so low in the reflectors as to change the distribution effects given by the reflector. For example, without the socket extenders with these shorter lamps, the spot of light on the ceiling, for the indirect system especially, was made smaller and correspondingly more brilliant. It was considered to be a point of interest in relation to the general problem to determine whether this comparatively small change in illumination effects would cause any difference in the eye's ability to hold its power to sustain clear seeing. The results of the tests for the different intensities of light for the three systems of lighting are shown in Chart II. Space need not be taken here to represent the comparative effects with and without socket extenders (see *Trans. Ill. Eng. Soc.*, 1915, X., pp. 473-476). In this connection it will be sufficient for our purpose here to state that quite an appreciable difference in result was obtained especially in case of the 25-watt lamps. These experiments constitute but one feature of a series conducted to show the effects of faulty installation.

2. *Semi-indirect Reflectors Differing in Density.*

In the work under the first and second sets of conditions the influence of differences in the distribution factors, more especially surface brightness, was clearly revealed by the use of wide variations in illumination effects. In the third set of conditions much smaller variations were employed. Such differences in effects were included as could be obtained by employing semi-indirect reflectors alone ranging from medium to dense. Six sets of reflectors were used, similar in size and shape and differing only in density. These reflectors were furnished by the Holophane Works of the General Electric Co. (now Ivanhoe-Regent Works) with special reference to the needs and purpose of the investigation. They are all of the bowl type and 8 inches in diameter. Reflector I. is a pressed Sudan toned brown; Reflector II. a blown white glass toned brown (an experimental product); Reflector III. a pressed Sudan; Reflector IV. a pressed Druid; Reflector V. a blown Veluria; and Reflector VI. a blown white glass (also an experimental product). Reflectors I., III., IV. and V. are commercial products, II. and VI. are in-

Lighting System : Semi-indirect.					Lighting System : Indirect.					Lighting System : Direct (8 Lamps).					Lighting System : Direct (16 Lamps).								
Foot Candles.					Foot Candles.					Foot Candles.					Foot Candles.								
Watts.	Volts.	cal.	zonal.	45°.	Watts.	Volts.	cal.	zonal.	45°.	Watts.	Volts.	cal.	zonal.	45°.	Watts.	Volts.	cal.	zonal.	45°.				
A	200	107	1.60	0.45	1.15	A	200	107	1.33	0.39	0.87	A	120	107	0.64	0.32	0.49	A	240	107	1.23	0.54	0.935
B	200	110	1.72	0.484	1.29	B	320	107	1.7	0.49	1.08	B	200	107	1.16	0.45	0.85	B	365	107	1.60	0.60	1.33
C	320	107	2.20	0.58	1.52	C	480	107	3.0	0.765	1.97	C	320	107	1.97	0.65	1.39	C	400	107	1.86	0.80	1.46
D	320	110	2.31	0.62	1.61	D	800	107	5.2	1.36	3.50	D	480	107	2.60	1.02	2.0	X	880	107	4.20	1.41	2.60
E	480	107	3.30	0.94	2.40																		
F	800	107	6.80	1.82	4.50																		
X	760	107	5.80	1.45	4.0																		

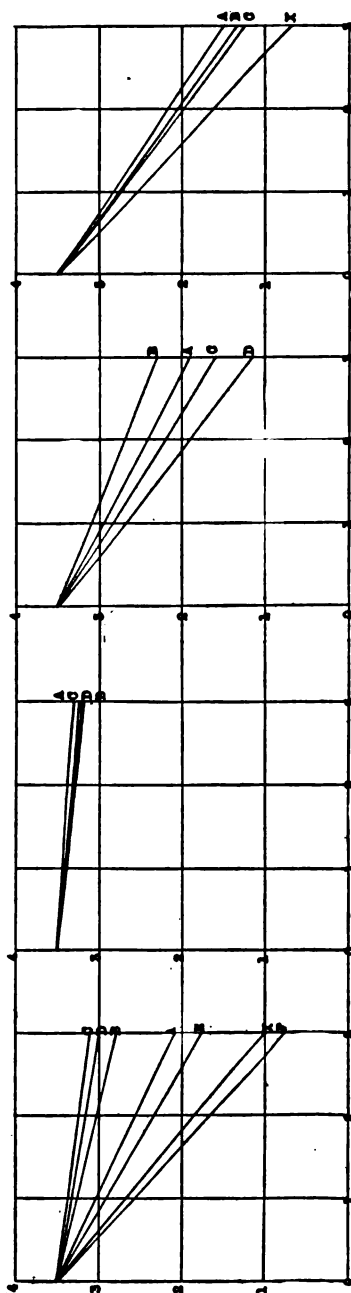


CHART II. (Direct, Semi-indirect and Indirect Systems of Lighting.) Showing the effect on power to sustain clear seeing of varying intensity of light for four installations of lighting: direct, semi-indirect and indirect systems, 8 lamps; and direct system, 16 lamps. Power to sustain clear seeing before and after work is represented on the ordinate and hours of work on the abscissa.

served in the series to give gradations in density. These reflectors were installed 30 inches from the ceiling in accord with the principles of indirect lighting. Clear tungsten lamps were used as light sources with each installation. These reflectors are numbered in order of their density from greatest to least, that is, Reflector I. is

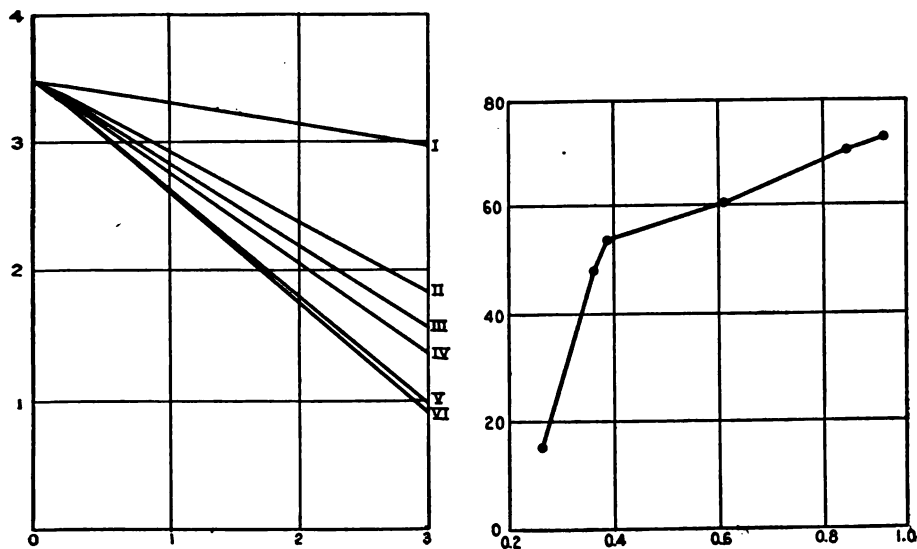


CHART III. (Semi-indirect Reflectors Differing in Density.) Showing the tendency of the six types of semi-indirect reflectors to cause loss of power to sustain clear seeing. In *A*, power to sustain clear seeing before and after work is represented on the ordinate and hours of work on the abscissa. In *B*, percentage of drop in power to sustain clear seeing after work for the different reflectors is plotted along the ordinate and brightness of reflector in candlepower per square inch along the abscissa.

Type of Reflector.	Volts.	Foot-candles.		45°.	Candle Power per Square Inch ⁵ .
		Vertical.	Horizontal.		
I	111	4.1	1.14	2.7	0.264
II	110	3.7	1.13	2.6	0.361
III	107.5	4.2	1.16	2.6	0.392
IV	105.5	3.8	1.15	2.5	0.614
V	105.5	3.7	1.15	2.6	0.848
VI	107.5	4.2	1.16	2.7	0.920

⁵ By multiplying the above values by 486.8 they may be converted into millilamberts, a term frequently used by engineers to specify small brightness quantities.

of the greatest and Reflector VI. is of the least density. In this connection it is scarcely needful to mention that the greater is the density of the reflector, the lower is the brilliancy of the surface which it presents to the eye. The results of this series of experiments are represented in Chart III.

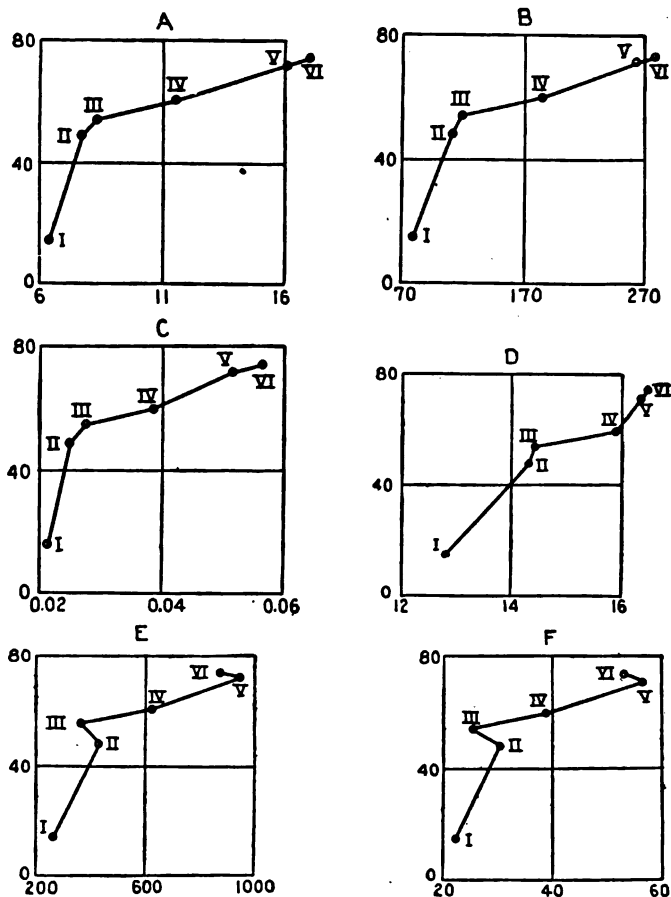


CHART IV. (Semi-indirect Reflectors Differing in Density.) Showing the tendency of the six types of semi-indirect reflector to cause loss of power to sustain clear seeing. In Curve A, percentage drop in power to sustain clear seeing after work for the different reflectors is plotted against ratio of average brightness to brightness at point of work; in B, against ratio of lightest surface to brightness at point of work; in C, against average brightness; in D, against ratio of lightest surface to average brightness; in E, against ratio of lightest surface to darkest surface; and in F, against ratio of average brightness to darkest surface.

In the tables referred to on a previous page (footnote 1, p. 445), we have shown for the sake of completeness of representation the gradation of surface brightness in three ways: (1) Brightness measurements of prominent surfaces have been made. (2) Ratios have been given between surfaces of the first, second, third, etc., order of brilliancy, and surfaces of the lowest order of brilliancy; and between surfaces of the first, second and third order of brilliancy and the brightness at the point of work. And (3) the mean variation from the average and the percentage of mean variation have been shown. In the consideration of these specifications a number of single items might be selected as of possible significance in relation to the effect on the eye. Among these may be mentioned the order of magnitude of the highest brilliancies; the average brilliancy; the ratio of the highest to the lowest order of brilliancy; the ratio of the highest order of brilliancy to the brilliancy at the point of work (brightness of test-object and reading page); etc. In order to see which of these correlate most closely with the results of the test, curves have been constructed in which some of these features are plotted against the results of the test. These curves are given in Charts III. and IV. In Chart III., *B*, percentage loss of visual efficiency is plotted against the highest order of brilliancy, namely the brightness of the reflector. In Chart IV. are grouped the remainder of the curves.

3. *Translucent Direct Reflectors Differing in Density.*

In the fourth series of experiments it was decided to use the same reflectors as were used in the third with one omission (the blown Veluria) because of its close similarity to another in the series, and to instal them in accord with the principles of direct lighting. In this series was included also a set of reflectors of prismatic glassware, differing somewhat from the others in size and design. They will be designated by the numerals I., II., III., IV., V. and VI., numbered for convenience of treatment in the tables in the order of their effect on the eye from best to worst. Reflector I. is the pressed Druid; Reflector II. the blown glass toned brown (experimental); Reflector III. the blown white glass (experimental); Reflector IV.

the pressed Sudan; Reflector V. the pressed Sudan toned brown; and Reflector VI. the prismatic. The size and type of the first five of these reflectors have already been given. Reflector VI. is of the extensive type, $8\frac{3}{4}$ in. in diameter and $5\frac{3}{4}$ in. deep. Reflectors I.,

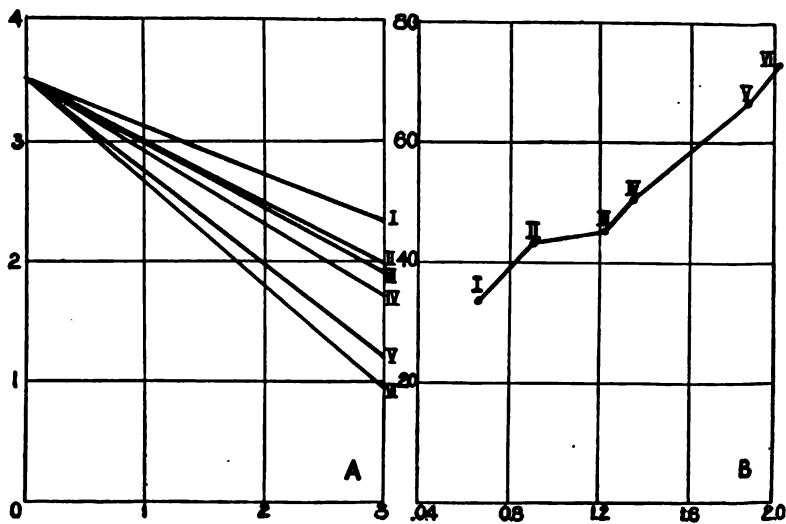


CHART V. (Translucent Direct Reflectors Differing in Density.) Showing the tendency of the six types of translucent direct reflectors to cause loss of power to sustain clear seeing. In *A*, power to sustain clear seeing before and after work is represented on the ordinate and hours of work on the abscissa; and in *B*, percentage drop in power to sustain clear seeing after work for the different reflectors is plotted along the ordinate and highest brightness of reflector in candlepower per square inch along the abscissa.

Reflector.	Volts.	Foot-candles.		45°.	Candle Power per Square Inch.
		Vertical.	Horizontal.		
Type I.	110	5.0	1.47	3.30	0.66
Type II.	113	4.84	1.43	3.35	0.924
Type III.	110	5.0	1.44	3.40	1.23
Type IV.	110.5	5.0	1.44	3.40	1.364
Type V.	111	4.80	1.44	3.30	1.87
Type VI.	107	5.10	1.47	3.40	2.05

IV., V. and VI. are commercial products, but II. and III. are experimental products inserted in the series to give gradations in density. The blown Veluria used in the former series of experiments was omitted from this series because the illumination effects obtained and

the effects on the eye, as determined in preliminary experiments, differed so little from those gotten from the blown white glass as to be considered as of little significance for the present work. These reflectors were all used with $2\frac{1}{4}$ in. form "H" holders, and were installed on the ceiling pendant in accord with the principles of direct lighting. Full-frosted tungsten lamps were used as light sources with each installation. The results of this series of experiments are represented in Chart V.²

In the tables³ referred to in footnote 1, p. 445, we have again

² In considering these results it should be borne in mind that these reflectors have been used to produce certain variations in illumination effects and that the work has not been conducted as a specific test of reflectors. For example, in order to secure in all cases approximately equal illumination at the test object, the lamps had to be operated at slightly higher voltages for some reflectors than for others. This produced for the different reflectors slightly different relative brightness values for outer surface and opening than would have been obtained had the lamps all been operated at the same voltage. Also clear and bowl-frosted lamps are more commonly used with these reflectors than full-frosted lamps. One effect of using clear or bowl-frosted lamps with them in this work would have been to have increased the brightness of both opening and outer surface of the reflectors and to have given, there is good reason to believe, a correspondingly uniformly poorer result for the eye. It is never entirely safe to predict results under conditions differing even slightly from what have been used, but from data at hand there is no reason to think that the change would have produced any significant difference in the relative rating of these reflectors. The full-frosted lamps were used for two reasons: (a) to test the whole group of reflectors under conditions as favorable as possible for the eye. This is admittedly only one point of view; the results might have had a more direct practical bearing had clear or bowl-frosted lamps been used. And (b), which is the chief reason, for the sake of making the work as far as possible comparable with the previous work, we desired to make the illumination of the test object as nearly equal as could be for the different reflectors, translucent and opaque, and equal to that used in the former work. This was best accomplished by the selection of lamps made.

³ The following points might perhaps be cited in connection with the brightness specifications given in these tables. In case of the translucent reflectors, installed pendant, two important items of surface brightness should be taken into account, the brightness of the opening and the brightness of the outer surface of the reflector. If a dense reflector is chosen, for example, the brightness of the opening tends to become excessively high; also its apparent or physiologic brightness is increased by induction from its dark surroundings which effect does not register on the photometer. If, on the other hand, the reflector chosen transmits too much light the brightness of the outer surface of the reflector becomes too high for the comfort and welfare of the

shown the gradation of surface brightness in the manner described in the preceding section. And in order to ascertain which of the brightness specifications—order of magnitude of highest brilliancy, average brilliancy, ratio of highest to lowest order of brilliancy, ratio of highest order of brilliancy to average brilliancy, ratio of average to lowest brilliancy, ratio of highest order of brilliancy to brightness at point of work (brightness of test object and reading page), etc.—correlate most closely with the results for the tendency to cause loss of power to sustain clear seeing, curves have been constructed in which a number of these features were plotted against the results of the tests. These curves are given in Charts V. and VI. In Chart V., *B*, per cent. loss in power to sustain clear seeing is plotted against the highest order of brilliancy that varies by any considerable amount from installation to installation, namely, the brightness of the reflector—outer surface and opening. In Chart VI. are grouped the remainder of the curves.

Three points may be noted perhaps with reference to these charts: (1) The prismatic reflectors, which differ in design from the rest of the series, more or less conspicuously fall out of the curve in every case but two. The effect of difference in design on the smoothness of the curve comes out especially in the results with the opaque reflectors (shown in the report of the next series of tests), in which case there are marked differences in both size and design. All of the curves plotted on the above bases are very irregular in case of these reflectors with the exception of separate curves for three which are similar in design. For a statement of the probable reasons for this inequality see this paper, pp. 468-9. (2) The greater regularity of the curves is rather strikingly marked in which the highest order of brilliancy that varies by considerable amounts or the ratios in which

eye. For the translucent reflectors used in these tests, the best results have been obtained with the reflectors of medium density. The reverse of this was true, it will be remembered, when the same reflectors were installed inverted. The highest brightnesses when these reflectors are installed pendant are the filament spots on the lamps. Only very small areas of these spots are visible, however, and their brightness and the brightness of the lamp differ so little from installation to installation as to be, in all probability, of relatively little consequence in a comparative study of effects on the eye. The significant variables are thus the brightnesses of the outer surface and opening of the reflector.

this quantity appears, is plotted against the results of the test. This, it will be remembered, was true also of the work of the preceding

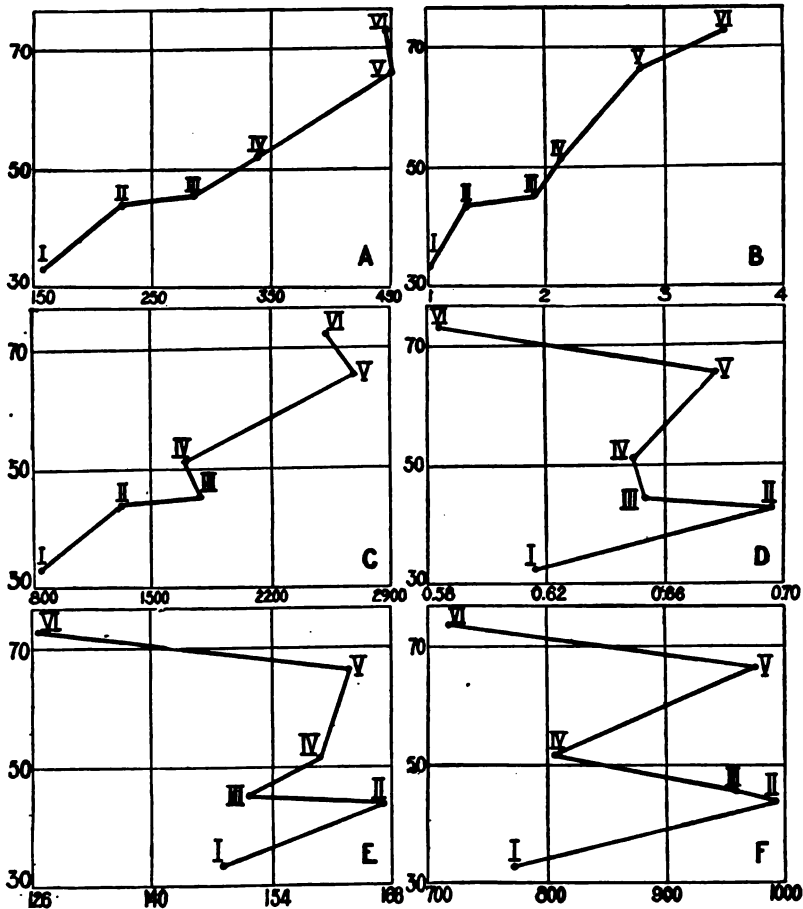


CHART VI. (Translucent Direct Reflectors Differing in Density.) Showing the tendency of the six types of translucent direct reflectors to cause loss of power to sustain clear seeing. In Curve *A*, percentage loss in power to sustain clear seeing after work is plotted against ratio of highest brightness of reflector to brightness at point of work; in *B*, against ratio of highest brightness of reflector to average brightness; in *C*, against ratio of highest brightness of reflector to darkest surface in field of view; in *D*, against average brightness; in *E*, against ratio of average brightness to brightness at point of work; and in *F*, against ratio of average brightness to darkest surface in the field of view.

experiments. (3) The range of brightness for this set of experiments is quite a little higher in the scale than for that of the former experiments with the same reflectors. This fact should be borne in mind, for example, in comparing the shape of the curves for the two sets of experiments in which highest order of brilliancy is plotted against the results of the tests. In case of the present experiments, for example, the curve begins at a point, 0.66 candle-power per square inch, which is well above the knee of the former curve. That is, the two curves are in general quite similar in shape when they are compared for the same range of brightness values. The former curve has, however, the greater regularity; but in connection with this fact it should be borne in mind that a variation of the brightness factor in separation can be more nearly accomplished with these reflectors when they are installed inverted than when they are installed pendant.

4. Opaque Direct Reflectors Differing in Dimensions, Lining and Design.

In this series of experiments the testing of pendant reflectors was continued. Seven totally opaque reflectors differing in lining, dimensions and design were used. In connection with the work of this series of reflectors, two points of perhaps more than usual interest may be noted: (a) By means of a modification of one of the reflectors used, Reflector IV., made to reduce the brilliancy of the opening, a field of view was given having the lowest maximum of brilliancy of any that we have as yet been able to obtain in an actual lighting situation; and (b) we were able to test more effectively than in any lighting situation previously used, the importance of evenness of surface brightness compared with evenness of illumination as a factor influencing the ability of the eye to maintain its power of clear and comfortable seeing.

The opaque reflectors represent a more promiscuous selection than the pendant translucent reflectors previously used. That is, in case of the translucent reflectors, all but one, Reflector VI., were of the same size and design, and the variations in the illumination effects were obtained by varying the density of the reflector alone;

while in case of the opaque reflectors the significant variations in the lighting effects were produced by changing the size (more especially the depth) of the reflector, the lining and the design. Of these Reflector IV. was of blown silvered glass with a system of spiral corrugations on its reflecting surface for the diffusion of light. This reflector was of the deep bowl type, $10\frac{1}{2}$ in. in diameter and $11\frac{1}{8}$ in. deep. Reflector V. was also of blown silvered glass and had a vertical system of finer corrugations than had Reflector IV. This reflector was $9\frac{3}{8}$ in. in diameter and 8 in. deep and was more distributing in type than was Reflector IV. Both of these reflectors were used with $3\frac{1}{4}$ in. form "A" holders. Reflector VI. was a steel, aluminum-finished reflector of the intensive type, $8\frac{1}{4}$ in. in diameter and $7\frac{1}{2}$ in. deep. This reflector was provided with a clip ring which was attached directly to the socket. Reflector VII. was a porcelain-enameled steel reflector of the shallow dome or distributing type, 15 in. in diameter and $6\frac{1}{4}$ in. deep. This reflector was used with a $2\frac{1}{4}$ in. form "O" holder.

Early in the work with these reflectors it was found that if good results for the eye were to be obtained with dense or completely opaque reflectors, some way must be gotten either of shielding the eye from the opening of the reflector or of reducing its brilliancy which increases as the density of the reflector is increased. Obviously something can be accomplished in this direction by using reflectors of the deep bowl type, giving specular rather than diffuse reflection, if the angle of presentation to the eye is not too great. Reflector IV., for example, is of this type. The opening of this reflector was of low brilliancy when viewed at an angle of $13^{\circ} 19'$, the angle of presentation to the eye for the two reflectors farthest from the observer in the present series of experiments. High up in the reflector, however, was a small but brilliant image of the lamp, a part of which was visible at an angle with the eye of $20^{\circ} 17'$, the angle made by the two reflectors at Outlet B (Fig. 1), and still more at an angle of 40° , the angle made by the two reflectors nearest the observer. It was thought advisable to find out how much this reflector could be improved in its effect on the eye by reducing the amount of reflection for a certain distance above the lower edge of the reflector. This was accomplished for the purpose of these ex-

periments by lining the reflector to a depth of 9.5 cm. (3.7 in.) with a mat surface of low reflection coefficient. This lining formed all of the surface that was visible in the openings of the four reflectors at Outlets *A* and *B*, and cut out the image of the lamp in the two reflectors at Outlet *B*. In the two reflectors nearest the observer, however, some of the bright lining and image were still visible, but the angle of presentation was here great enough that comparatively little effect on the comfort of the eye and its power to sustain clear seeing was had or was to be expected. Two sets of lining were used, one a very dark gray (reflection coefficient of about 4 per cent.); the other a lighter gray (reflection coefficient of about 38.5 per cent.). Reflector IV. provided with the first of these linings is designated in the charts as Reflector I., and with the second, as Reflector II. Still another modification was made of this reflector to lessen the effect of the opening on the eye. The apparent or physiologic brightness of this opening, as was the case with the other opaque reflectors, was enhanced by induction from the dark green coating or backing on the outer surface of the reflector. This effect is quite noticeable on inspection where a comparison with a reflector presenting less or no induction is afforded, but does not register in the photometer because the surroundings are not included in the photometric field. In case of Reflectors I. and II. this induction was lessened a great deal by covering the outside of the reflector with a closely fitting cap of mat white paper.

Because of the favorable results obtained with these modified reflectors, a similar modification of Reflector V, was made by the manufacturer for the purpose of reducing the brilliancy of its opening. In this case the band was made permanent by sand-blasting the corrugated glass surface of the reflector. The coefficient of reflection of the surface thus prepared was approximately 52 per cent. The band was made 5 cm. in width. While considerable improvement in the effect on the eye was produced by this modification, not nearly so good results were gotten as in the other case because (*a*) the coefficient of reflection was not sufficiently reduced by the sand blasting; and (*b*) Reflector V. was not deep enough to give the best results with this type of modification. The tip of the lamp, for example, was visible to the observer in case of four out of the six

reflectors in the field of view. This reflector is designated in the charts as Reflector III. All of the reflectors of this series were installed on the ceiling pendant in accord with the principles of direct lighting.

It was our wish to conduct this investigation, as has been the case in all of our work on the distribution factors, with the color value and the intensity of light as nearly equal as possible at the test object. Clear tungsten lamps were used with Reflectors I., II. and IV.; full-frosted lamps with Reflectors VI. and VII.; and bowl-frosted lamps with Reflectors III. and V. Clear lamps were used in the cases mentioned because in the first place in reflectors of this type the lamps were not visible to the observer at the point of work; and secondly, although the illumination given was high in the average, the distribution was such as to give a low illumination at the point of work. That is, the tendency of these reflectors, installed at the height used in our test room, was to give lanes of light directly beneath the two rows of reflectors, shading off to a correspondingly low value on either side. Full frosted lamps were used with Reflectors VI. and VII., because with Reflector VI. a part and with Reflector VII. all of the filament would otherwise have been visible to the observer; also the value of the illumination at the test object would have been much too high as compared with the other reflectors in the series and higher than the values used in previous work. In case of Reflectors III. and V. both of the above objects, namely, the better protection of the eye from the filament and the performance of the tests with the illumination values as nearly as possible equal to those obtained with the other reflectors and in previous work, was best accomplished by the use of bowl frosted lamps.

The results of this series of tests are represented in Chart VII. Again in order to ascertain which of the brightness specifications—order of magnitude of highest brilliancy; average brilliancy; ratio of highest to lowest order of brilliancy; ratio of highest order of brilliancy to average brilliancy; ratio of average to lowest brilliancy; ratio of highest order of brilliancy to brightness at point of work (brightness of test object and reading page); etc.—correlate most closely with the results for the tendency to cause loss of power to sustain clear seeing, charts were constructed in which a number of

these features were plotted against the results of the tests. As compared with the corresponding charts given for the previous experiments, these charts show great irregularity unless separate curves

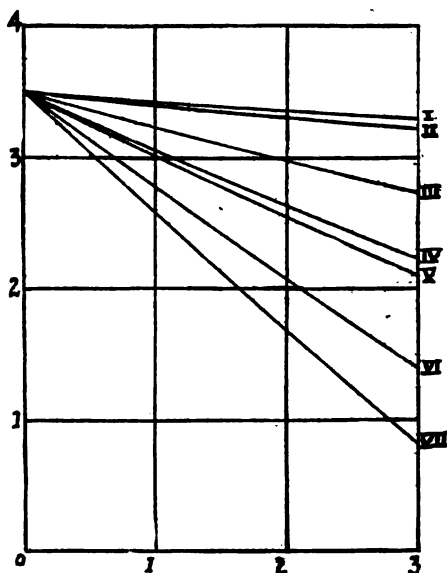


CHART VII. (Opaque Direct Reflectors Differing in Lining, Dimensions and Design.) Showing the tendency of the seven types of opaque direct reflectors to cause loss of power to sustain clear seeing. Loss of power to sustain clear seeing before and after work is represented on the ordinate and hours of work on the abscissa.

Reflector.	Volts.	Foot-candles.		45°.
		Vertical.	Horizontal.	
Type I.....	111	2.25	0.72	1.66
Type II.....	111	2.90	0.90	1.95
Type III.....	107	4.25	1.19	2.95
Type IV.....	109	3.42	1.18	2.40
Type V.....	107	4.30	1.21	3.00
Type VI.....	112	4.70	1.42	3.30
Type VII.....	109	4.90	1.47	3.30

are plotted for the reflectors similar in design. Reasons for the irregularity are, perhaps, (a) the method of specifying brightness. We are inclined to believe that if the surfaces of high brilliancy which vary considerably in extent for the series of reflectors se-

lected, were given in total candlepower instead of candlepower per square inch, they and the ratios based on them would correlate more closely with the effects on the eye. That is, it is a well known law in physiological optics that an increase in the area of a bright surface functions to a certain extent as an increase in its brightness. The opening of Reflector VII., for example, which gives the poorest results for the eye, has a lower intrinsic brightness than has the opening of Reflector VI.; but a great deal more of it is visible to the observer, also a great deal more of the lamp. When the surfaces in question differ in area to any very great extent, it is obvious that a measurement in candlepower per square inch is not an adequate specification when effects on the eye are to be considered. The total value in candlepower would be much more representative of the comparative power of these surfaces to affect the eye. (b) The angle of presentation to the eye. The openings of the different types of reflector differed in their distances above the working plane, although installed on the ceiling in every case. And (c) the number of factors varied. Brightness is not the only one of the distribution factors varied by considerable amounts by the different types of reflector. Because of the irregularities shown by these curves, space has not been taken to represent them here.

For all the conditions represented in this and preceding sections the work of testing was completed by determining for the different types of reflectors the relative tendencies to produce ocular discomfort as was noted in our introductory chapter. Two cases were made of this determination—one with the eye at rest, maintaining no particular adjustment, and the other when it was at work. Space has not been taken here for a statement of the results of these determinations. They are given in tabular form,⁴ with a comparison in per cent. of the mean error of the determination and the change produced by changing the conditions tested, in the references appended below. In these tables are included also for the sake of comparison results expressing the tendency of each type of reflector to cause loss of ability to sustain clear seeing. A high correlation was

⁴ *Transactions of the Illuminating Engineering Society*, 1915, X., pp. 497-500; 1915, X., pp. 1114-1116; 1916, XI., pp. 1129-1131; 1917, XII., pp. 477-479. PROC. AMER. PHIL. SOC., VOL. LVII, PP. 24, 1918.

found to obtain in each case between the tendency to produce ocular discomfort and to cause loss in power to sustain clear seeing.

As was stated earlier in the paper a marked characteristic of the effects produced by the dense and completely opaque direct reflectors was the low illumination of the ceiling and the upper part of the room, and the high and in some cases almost glaring illumination of the floor and objects in the working plane. So far as effects on the eye of the kind registered by our tests are concerned, however, these irregularities of illumination and of the low surface brightnesses extraneous to the lamp and reflector seem to be of comparatively little consequence so long as the higher brilliancies of lamp and reflector are themselves taken care of. In this series of experiments, including the translucent direct reflectors, we have had quite wide variations in the distribution of illumination, ranging from well-illuminated ceilings and comparatively evenly illuminated walls and working plane for the direct reflectors of medium density to the dark ceilings and upper parts of the room and highly illuminated lower half in case of the opaque reflectors. And considering this work in connection with the preceding work, by means of the opaque and translucent reflectors turned both up and down, and reflectors of the distributing and focusing types, we have had the greatest amount of light first in the upper half of the room, then in the lower half, and within limits lanes of light have been produced; still it has been possible to get in all of these cases comparatively good effects on the eye so long as no excessive brilliancies were introduced into the field of view. Table I., for example, has been prepared to show the difference in the evenness of the illumination on the working plane for Reflector I. of the series of translucent direct reflectors (designated in the table as Reflector *A*) and Reflectors II. and IV. of the present series of opaque reflectors; and Chart VIII., Fig. 1, to give a graphic representation of the eye's ability to sustain clear seeing for these reflectors and Reflector I. of the present series. (The distribution of illumination for Reflector I. was so similar to that for Reflector II. that it has been omitted from Table I.). A comparison of this table and chart shows the following points. Reflector *A* gives a comparatively even illumination not only of the working plane but of the entire room, and Reflectors I. and II. a very

TABLE I.

SHOWING A COMPARISON OF THE EVENNESS OF ILLUMINATION FOR REFLECTOR A (I. OF THE TRANSLUCENT DIRECT SERIES) AND I. AND II. OF THE OPAQUE DIRECT SERIES.

Reflector A gives a comparatively even illumination and Reflector II. a very uneven illumination; yet Reflector II., from which all high brilliancies have been eliminated, gives much better results for the eye, so far as tendency to produce discomfort and power to sustain clear seeing are concerned, than Reflector A. Furthermore, Reflector IV., which gives the same general type of distribution of illumination as Reflector II., but has not had the brilliancy of its opening cut down, gives poorer results for the eye than Reflector A. Reflector II., it will be remembered, is Reflector IV. modified so as to reduce the brilliancy of its opening. In this table, the results are arranged just as the stations occur in the test room. (See Fig. 1, Plan of Test Room.) Space has been taken here for a comparison only of the vertical components of illumination for the three reflectors.

Reflector Type A.										Reflector Type II.										Reflector Type IV.									
1.40	3.1	3.5	3.1	3.0	3.4	3.0				0.58	5.7	6.6	1.93	1.31	4.35	3.2				0.58	2.8	5.0	2.3	1.73	6.2	4.0			
4.3	5.2	4.7	4.3	4.9	3.8					7.8	6.5	3.7	3.0	10.8	6.4					7.6	5.85	5.08	4.1	9.1	7.8				
4.7	5.5	4.9	4.6	5.4	4.5					5.4	7.1	2.8	2.85	10.0	7.1					5.8	8.8	4.65	3.68	10.8	8.4				
2.3	4.7	5.5	5.38	5.0	5.5	4.8				1.25	6.8	5.6	3.9	3.7	5.6	6.7			1.23	6.4	5.2	5.8	5.5	5.9	8.1				
2.65	4.7	5.8	5.2	5.2	6.0	5.0				1.17	6.0	8.8	4.2	3.2	8.7	6.6			1.23	5.36	9.5	4.6	3.9	11.2	6.8				
3.2	5.1	6.1	5.4	5.3	5.9	4.85				1.10	5.8	5.1	5.3	3.75	5.8	6.95			1.54	7.1	5.2	5.4	4.3	8.2	7.8				
2.8	5.1	6.0	5.4	5.1	5.6	4.75	3.3			1.12	5.8	9.5	3.9	3.0	8.8	4.2		1.4	1.48	5.8	10.8	4.3	4.8	13.2	6.5				
2.38	4.25	5.2	4.4	4.1	4.60	3.7	2.55			1.37	7.4	5.3	5.9	3.5	7.2	6.4		1.25	1.7	7.6	4.6	5.82	6.65	5.2	9.6				
1.96	3.2	3.5	3.0	3.2	3.2	2.75				0.99	4.8	7.8	3.25	2.12	5.8	3.12			1.04	4.0	7.0	2.8	3.1	8.9	4.6				
1.68	1.75	1.5								0.56	0.92	1.18							0.51	1.01	1.27								

uneven illumination; yet Reflectors I. and II., from which all high brilliancies have been eliminated, give very much better results for the eye than Reflector *A* so far as the power to sustain clear and comfortable seeing is concerned; and Reflector IV., which gives the same general type of distribution of illumination as Reflectors I. and II. but has not had the brilliancy of its opening cut down, gives

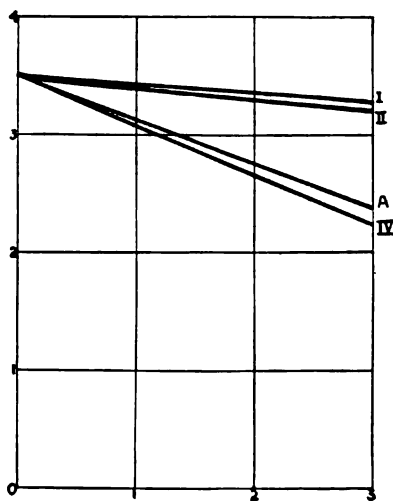


CHART VIII.

FIG. 1. Showing a comparison of the effects of unevenness of illumination and unevenness of surface brightness on the power of the eye to sustain clear seeing for a period of work. Reflectors I., II. and IV. give a very uneven illumination (dark upper walls and ceiling and lanes of light in the working plane); but the brightness of the openings of Reflectors I. and II. have been reduced by lining Reflector IV. to a depth of 9.5 cm. with surfaces of low reflection coefficient, 4 per cent. and 38.5 per cent. respectively. *A* is a translucent reflector giving a comparatively even illumination of walls, ceiling and working plane. All are installed pendant in accord with the principles of direct lighting.

poorer results for the eye than Reflector *A*. The results for Reflectors I., II. and IV. were taken from a series in which an attempt was made to find the maximum brightness of opening which the eye could stand without much loss in power to sustain clear and comfortable seeing with the types of reflector and installation used. The effect on the eye of Reflector I. (coefficient of reflection of

lower edge, 4 per cent.) differs very little, it will be observed, from that of Reflector II. (coefficient of reflection of lower edge, 38.5 per cent.). Any increase of the value of this coefficient above 38.5 per cent., however, caused a much more rapid change in result.

It may be of interest to append at this point another chart, Chart VIII., Fig. 2. In this chart are represented the best results we have as yet been able to obtain with the different types of translucent and

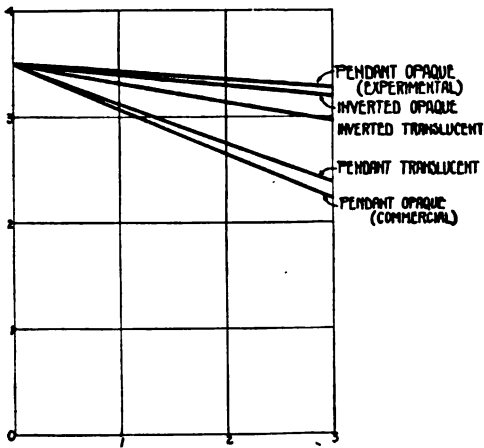


FIG. 2. Showing a comparison of the best effects we have been able to obtain with different types of lighting. The installations which have caused the least loss in power to sustain clear seeing are the ones which give the lowest maximum brilliancy in the field of view.

opaque reflectors installed pendant and inverted. From this chart it will be seen that comparatively good results may be gotten with both pendant and inverted reflectors. In general, however, the work has shown that the problem of protecting the eye from excessive brilliancies and of producing at the same time a satisfactory evenness of illumination presents greater difficulty in case of the pendant than in case of the inverted reflectors and has apparently been less adequately dealt with thus far in the work of reflector designing.

III. OTHER INVESTIGATIONS PERTAINING TO THE HYGIENIC EMPLOYMENT OF THE EYE.

These include the effect of different types of eye-shades under different conditions of lighting; the effect of different conditions of

lighting on the extrinsic muscles of the eye; the effect of the angle at which the light falls on the work; the effect of motion pictures; etc. Space can not be taken in this paper for a detailed report of these investigations. For convenience of reference a complete bibliography of the studies published up to the present time is appended at the end of the paper.

IV. OCULAR DISCOMFORT IN RELATION TO THE POSITION OF THE SOURCE OF LIGHT IN THE FIELD OF VIEW.

In addition to studying the conditions that give us maximal visual efficiency or power to sustain clear seeing, it is important also to determine the lighting conditions and eye factors that cause ocular discomfort. Therefore, in case of each of the lighting situations tested for tendency to cause loss in power to sustain clear seeing, we have determined the tendency to produce ocular discomfort, as has been noted in the preceding pages. In the work on the lighting systems previously described, however, the effect of the angle of presentation of surfaces of high brilliancy (lamp, surfaces and openings of reflector, ceiling spots, etc.) on both the power to sustain clear seeing and the tendency to produce ocular discomfort was shown through a comparatively small range of variation of angle. It was thought advisable to supplement this work by determining the effect on the tendency to produce ocular discomfort for a wider range of variation of angle of presentation. For this purpose a large perimeter was used, along the arm of which the brilliant surface, the effect of which was to be determined, could be moved. A variable area of brilliant surface was obtained by mounting on the arm of the perimeter a lamp house in the side of which next to the observer's eye a large iris diaphragm was inserted. The brilliancy and color value of this test surface could be varied within limits to suit the needs of the experiment by means of absorption screens and filters. Larger variations of intensity were obtained by means of the use of lamps of different wattages. The arm of the perimeter could be shifted to any meridian in which it was desired to work and the lamp could be moved at will along the arm. Working in this way it is possible to investigate the effects of many types of distribution

of surface brilliancy in the field of view and many variations of intensity and color value. Of these variations the results of only one will be given here, namely, the exposure of the brilliant surface at different points in the field of view for one eye when fixation and accommodation were taken for a point at a distance of one meter.

In carrying out the investigation the following precautions were observed. (a) It was found better to work in a room moderately illuminated by a source of light behind the observer and entirely concealed from him, rather than in the dark room. The intervals of dark adaptation between exposures in the dark room seemed to make the observer's eye too sensitive for our purpose. This was especially true for certain parts of the periphery of the field of view. In becoming supersensitive there was a tendency to become erratically sensitive. (b) It was found that blinking serves as a variable factor for the relief of discomfort and that the amount of blinking must be made constant from test to test. This was accomplished by having the observer blink at equal intervals during the exposure, timing himself by the stroke of a metronome. The interval most natural and suitable for this purpose was determined for each observer separately. (c) All comparisons were planned in series. For example, if it were desired to compare the sensitivity for the temporal and nasal halves of the field of view in a given meridian, the exposure was made first at one point in one half and next at the corresponding point in the other half and the order of giving them was changed. This was to guarantee that the eye should be as nearly in the same condition with regard to progressive fatigue, etc., as was possible. Further to safeguard against error in this regard, series were compared in which the exposures were repeated in the reverse order. (d) An interval of recovery was allowed between exposures. This interval had to be determined separately for each observer and often had to be made different for the same observer on different days. It was never changed, however, during the course of a series, the results of which were to be compared. (e) In order that the observer's head be held rigidly in position during the exposure, he was required to bite an impression of his teeth previously made and hardened in wax on a mouthboard. (f) As has been the case in all of this work, care has been exercised in the choice of observers to

select only those who had already shown a satisfactory degree of precision in other work in physiological optics and whose clinic record showed no uncorrected defects of consequence. All were under thirty years of age. Before being allowed to take part in the actual work the results of which were used in the comparative study, each observer was trained to a satisfactory degree of precision in a preliminary series of tests with the light exposed at several points in the field of view. In the actual work of testing the results were compiled from a number of observations and the precision was checked up by the size of the mean variation. No results were accepted as significant unless the variation produced by changing the position of the source in the field of view was largely in excess of the mean variation or mean error for each position tested. When an exposure was to be made, the fixation was taken, the light turned on and a record was made by the observer on a kymograph of the time that was required for just noticeable discomfort to be set up; or, if it were desired, when the different stages of discomfort were reached. The judgment was found to present no special difficulty and the method, when properly applied, to provide a feasible means for comparing the sensitivity of the eye to discomfort under all the conditions to which we have been able thus far to extend its application. In actual practice the method also brings out an analysis of ocular discomfort.

Ocular discomfort seems to be a complex of three experiences each of which develops at a different time. When the light is turned on, we have at once glare. This is a light sensation and though unpleasant has no painful elements. Next comes a conjunctival sensation which begins with what is commonly called "sandiness" and soon passed over into a sharp, stinging, stabbing pain. Lastly there is what is probably a muscular discomfort, a hurting and aching in the ball of the eye which, if the exposure is continued long enough, seems to radiate to the socket and the surrounding regions of the face and head, the arch of the brow, the forehead, the temples, etc.

The comparative determinations were made in 12 meridians of the field of view from the center to the limit of vision in the given meridian at points separated by 15 degrees. Space will be taken here only for a general statement of result. In general for all of our ob-

servers, with the exception of two meridians for one observer, the point of maximal sensitivity to discomfort was out of the center of the retina; the nasal half of the retina was more sensitive than the temporal half and the upper half more sensitive than the lower. In passing from the center to the periphery of the retina, the sensitivity is found first to increase and then to decrease, becoming extremely little at the limits of the field of vision. In the horizontal meridians both on the temporal and nasal sides, maximal sensitivity is found around and in the region included between 15° – 45° ; in the vertical meridians, around and in the region included between 15° and 30° .

V. THE EFFECT OF DIFFERENT ILLUMINANTS ON THE POWER OF THE EYE TO SUSTAIN CLEAR AND COMFORTABLE SEEING.

In the work as conducted up to the present time a study has been made of the effect on the eye of differences in the way in which the light is delivered to it from a given type of illuminant. In work now in progress, a series of similar studies is being made of the illuminant itself. Different illuminants are being used with the same conditions of installation, shading, etc., and a correlation is being made between the lighting effects obtained and the power to sustain clear and comfortable seeing. As the tests are being conducted, color value is the only variable present of any magnitude from illuminant to illuminant. The tests so far as completed show that color value, while not exercising so important an influence as improper and inadequate shading on the power of the eye to sustain clear and comfortable seeing in lighting conditions as we have them in current practice, is a factor that should not be ignored in the work that is being done in the interests of the conservation of vision.

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BRYN MAWR COLLEGE,
April, 1917.

SYMPOSIUM ON FOOD PROBLEMS IN RELATION TO THE WAR.

I.

PHYSIOLOGICAL EFFECTS OF A PROLONGED REDUC- TION IN DIET ON TWENTY-FIVE MEN.¹

By FRANCIS G. BENEDICT.

(Read April 20, 1918.)

I am privileged this afternoon to discuss the subject of food conservation from a point of view based upon an extensive research made in conjunction with Drs. Walter R. Miles, Paul Roth, and H. Monmouth Smith. The details will shortly be published in a monograph by the Carnegie Institution of Washington.

It is perhaps remarkable that with all the current discussion regarding food conservation so little emphasis has been laid upon the possibility of conserving food by reducing the diet. When one recalls the agitation of enthusiasts for reduced diets during the past thirty years and recognizes the fact that all special, pet theories can, at this psychological moment, obtain a better hearing than at any previous time, it is surprising that the advocates of reduced diet have made so little progress and, indeed, have apparently ceased their propaganda.

The popular conception that we eat too much is usually quantitatively expressed by the statement that we eat "twice as much as we ought." The Nutrition Laboratory has for years been endeavoring to discover if there exist any special groups of individuals who live regularly upon a diet that would be commensurately low. For this purpose it was assumed that the minimum or basal metabolism must be taken as the index of food requirement. Differences in muscular activity are so great that no two individuals can be

¹ From the Nutrition Laboratory of the Carnegie Institution of Washington, Boston, Massachusetts.

compared save on an absolute quiescent, resting basis. After the metabolism of 200 or more individuals had been carefully measured, it was seen that, although we were dealing with people of varying ages, dietetic habits, and supposedly very low metabolism, no such individuals were easily recognized in our measurements. It would thus appear, offhand, that if there are no individuals other than pathological, which present abnormally low basal metabolism and if the law of conservation of energy in the human body obtains, as we know it does, then there is no *a priori* reason for expecting that a reduced diet can be permanently adhered to. A reduction in diet will simply mean that body reserves will be drawn upon until death from starvation occurs.

About a year ago I had the privilege of lunching with Professor Alonzo E. Taylor in Philadelphia, when I received at first hand information regarding some of his important observations in Germany on the dietetic habits of the German civilian population. While there was no quantitative measurement of the food intake of these people, the fact appeared to be established without doubt that the Germans were subsisting upon a very low calorie intake and that this had endured for so long a time since the beginning of the war that it seemed highly probable that the former liberal body reserves no longer supplemented the diet. As a result of this conference a previously formed plan was crystallized into definite action. After conference with my colleagues at the Nutrition Laboratory, an extensive research upon the influence of a prolonged reduction in diet on a group of men was outlined. Obviously much profit was derived from the criticisms of the historic research of Professor Chittenden with his group of soldiers. Professor Chittenden's problem dealt mainly with the nitrogen intake and output, but when the energy of the diet comes into discussion, it is clear that the dietetic control must be even more rigid and one must, in the last analysis, be wholly dependent upon the personal integrity and veracity of the subjects. If a person ate more protein than was allowed, this would show in the urine. A person could eat considerably more calories than actually allowed and yet no direct chemical control could be secured.

Through the kind offices of Professors J. H. McCurdy and

Elmer Berry, of the International Y. M. C. A. College at Springfield, Massachusetts, both unusually interested in metabolism problems, arrangements were made to select twelve men out of a group of volunteers from the student body. The men entered heartily into the spirit of the whole research and readily consented to all the strict requirements of the test. It is a great pleasure to record that during the four months of experimenting there was not the slightest indication of any of these men wittingly or unwittingly violating even the strictest regulations of the research. The honor system obtains at the College; the men realized that they were in a position to do the nation a great service and with the fidelity, enthusiasm, and high ethical spirit exhibited by the whole student body, these men went through the arduous four months without a serious complaint.

The general plan was to curtail the diet sufficiently to reduce the weight approximately 10 per cent. This could have been done by a complete withdrawal of food for about 14 or 15 days. It was recognized that these men were, first, college students with obligations for educational advancement and, second, volunteers for scientific research. A complete fast for 14 days would, in all probability, have caused most of them considerable discomfort, if not distress. The alternative was to curtail the dietetic intake so that the weight loss would take place, not in 14 days, but in 4 to 6 weeks. This was done by serving the men approximately one half to two thirds of the caloric requirements prior to the dietetic control, making absolutely no change in the kinds of foods eaten. The men were cautioned not to lessen their mental or physical activities. Obviously if the activity of a group of men were lessened as, for instance, by putting them to bed, to use an extreme illustration, their dietetic requirements would be very much less. Suffice it to say that these men carried out all the requirements of collegiate activity, both physical and intellectual, throughout the entire period. As soon as the reduction in weight had reached 10 per cent. or thereabouts, the calories in the intake were increased to such an extent as to hold the weight at a constant level. The number of calories required to hold this weight constant over a considerable period of time could be taken as a fair representation of the actual caloric requirement for this group of men.

At the start we were confronted with the possibility of a seasonal variation. Thus, if one took a group of twelve active Y. M. C. A. students, at the end of a summer vacation, fresh from summer camps with their outdoor activities, and placed them in academic halls with restricted hours, artificial illumination, and curtailed physical activity, it is conceivable that there would be a normal retardation of metabolism in the later fall months. To insure a suitable base line, therefore, a second group of twelve men from the large number of volunteers originally presenting themselves were selected to act as a control squad. These men were in every particular studied with the same degree of care as Squad A, except that there was no dietetic control.

While body-weight can be taken as an approximate index of the metabolic level, further checks were absolutely necessary to rule out the inevitable difference in muscular activity that would be found with groups of individuals, even when they were subsisting under the same collegiate conditions. The gaseous metabolism was therefore measured practically every morning for each one of the first squad. These measurements were made by collecting the expired air and analyzing it. From the amounts of oxygen consumed and carbon dioxide produced the basal heat output could be computed by indirect calorimetry, thus furnishing the second index of metabolic level. The pulse rate was recorded simultaneously every morning. Every other Saturday night the entire group of men were taken to Boston and placed inside a large respiration chamber, where they could sleep comfortably. The carbon-dioxide excretion of the twelve men was thus determined simultaneously during deep sleep. This furnished a third criterion for judging the metabolic level.

The control squad showed no seasonal variation and their basal metabolism, as measured in the large respiration chamber in Boston, was found to be absolutely identical with that of the first group of twelve men prior to the restriction in diet. To check the important findings with the first squad during the early period of the investigation, the second squad was later placed upon a very restricted diet for a period of three weeks, the diet given being less than one half of their normal requirements.

For both squads, when on diet, the food for each day was care-

fully weighed, sampled, and analyzed for the individual men. It is thus possible for us to measure the complete intake of protein and calories. The urine was collected throughout the entire time, and the feces at frequent intervals. It is a tribute to the painstaking and conscientious coöperation of these men that throughout the entire period of four months the urine was rarely lost. We thus have complete data for striking a balance between the nitrogen in the food and the nitrogen in urine and feces.

Advantage was taken of each bi-weekly visit of the separate squads to the Laboratory in Boston to put them through 17 psychophysiological tests. Although it was rather difficult to secure much evidence of introspection without the danger of suggestion, careful records of all the relevant observations on introspection were made.

The most important scientific findings may be summed up as follows:

1. A gradual reduction in weight to a point 12 per cent. below the initial weight took place during a period of from 3 to 10 weeks, with low calories and a moderate amount of protein in the food intake. The normal demand of the men prior to the dietetic alteration ranged from 3,200 to 3,600 net calories. One squad of 12 men subsisted for three weeks on 1,400 net calories without special disturbance.

2. After the loss in weight of 12 per cent. had been reached, the net calories required to maintain this weight averaged about 2,300, or approximately one third less than the original amount required.

3. At the end of the reduction in weight the actual heat output during the hours of sleep, as computed by indirect calorimetry, was approximately one fourth less than normal, thus giving a rough confirmation of the lowered number of calories found by actual measurement of the food intake. That there was no pronounced seasonal variation in metabolism was shown by the uniformity of the metabolic level of the control squad (Squad B).

4. The heat output by indirect calorimetry per kilogram of body-weight and per square meter of body surface was essentially 18 per cent. lower than at the beginning of the study.

5. Throughout the period of loss in weight and for some time subsequent thereto, there was a pronounced loss of body nitrogen.

In round numbers these men each lost approximately 150 grams of nitrogen. There is an intimate relationship between this "surplus nitrogen" and the metabolic level. Removing the "surplus nitrogen," we believe, distinctly lowers the stimulus to cellular activity.

6. The urine nitrogen per day at the maintenance diet of 2,300 net calories was about 9 grams. The control group of 12 men, living substantially the same life and eating in the same dining room, but with unrestricted diet, showed a nitrogen output of 16 or 17 grams per day.

7. The pulse rate was astonishingly lowered. Many of the men showed morning pulse rates as low as 33 and daily counts of 32, 31, and 30 were obtained; at least one subject gave six definite counts on one morning of 29.

8. The blood pressure, both systolic and diastolic, was distinctly lowered.

9. The skin temperature, as measured on the surface of the hands and forehead, was, with some subjects, considerably lower than normal. With most of the men normal temperatures prevailed.

10. The rectal temperature was practically normal.

My colleague, Dr. Walter R. Miles, found as a result of numerous tests of the neuro-muscular processes that there was no striking change as a result of the reduced diet. There was a very slight falling off in the strength tests with the hand dynamometer.

As one of the best indices of muscular performance my associate, Dr. H. Monmouth Smith, measured the energy required by each man to walk 1 mile in about 20 minutes. With a reduced diet, the requirement was found to be lower with all the men than with a normal diet, this being due, in part, to the fact that the reduced weight meant a lower weight to transport. In other words, these men walked a mile with noticeably less energy consumption than a man not subsisting on a reduced diet.

The subjective impressions were almost uniform that the muscles in the thigh were distinctly weakened. The men complained of difficulty in walking upstairs, but our personal observations go a long way toward refuting this, for all the men seemed able to go upstairs two steps at a jump on several occasions. On February 1, 1918, at Springfield, after 4 months on diet, eleven of the diet

squad were pitted against eleven men from the college body in an arm-holding contest for endurance. The arms were held extended, palms down, at the level of the shoulder. The number of men falling out were practically the same in both squads; as a matter of fact, 7 in the diet squad and 8 in the uncontrolled squad held their arms out for one full hour.

Two of the men had chronic bad noses. One was operated upon during the test and the other should have been. Aside from these two, the prevalence of colds during the period was about the same as with the other college students. During the study three men underwent ether narcosis for operations (on nose, foot, and hemorrhoids) and made rapid recoveries. One man at the lowest period of weight contracted what was diagnosed by three physicians as typhoid fever, although the final course of the disease seemed to leave the diagnosis somewhat in doubt. He ran through a very high fever, and was critically ill for some time, but has made a complete convalescence and recovery and has returned to college.

The most noticeable discomfort experienced by the subjects was a feeling of cold, which it is only fair to say might be due in large part to the severity of the past winter. In general, notwithstanding the very great reduction in the metabolism, which we believe was due to the removal from the body of the stimulus to cellular activity of approximately 150 grams of "surplus nitrogen," the whole period of lowered food intake had no untoward effect upon the physical or mental activities, and the men were able to continue successfully their college duties.

When the second squad was put upon a restricted diet, the picture exhibited by the first squad was strikingly duplicated in all details, although, as the loss in weight was obviously not so great with the second squad (6 per cent. as compared with 12 per cent.) the phenomena were quantitatively somewhat less emphasized.

At the conclusion of the entire research the men presented an appearance not unlike the average college student; it would have been difficult to pick them out from the rest of the college body on the campus. On close inspection the members of the diet squad would perhaps have appeared somewhat emaciated, particularly in the face, but they were performing their duties as college students,

both physically and intellectually, with no obvious reduction in stamina. No words can express their exact condition at the end of these tests so clearly as a short section of motion-picture film, showing the general agility, spirit, and physical ability of these men.

The great objection to making practical deductions from laboratory experiments is usually that such researches are carried out on the lower animals, or if men are studied but one or at the most two men are used. With a group of twenty-five men, such as was studied in this research, one is justified, if ever, in drawing deductions or making recommendations. In addition to the fact that we have experimental evidence based upon twenty-five men from which to draw conclusions, we have also the fact that this is a period of stress, a period of innovation, a period for trial, for experimentation, for "taking chances," if you will. These combined factors are based, first, upon the large human experience of enforced diet restriction in Germany, second, upon the psychological set of the patriot and, third, upon the moral obligation laid upon us all to contribute to the vast project of food conservation. We cannot then be charged with faddism or irrational propaganda if we are led to make certain definite recommendations—recommendations that admittedly we would never make in peace times and that admittedly may have serious faults. These recommendations are primarily a war measure. In time of peace and plenty, the physician would rightly caution against an undue adjustment of the diet or fundamental alteration in dietetic habits. Still, when millions of our allies and hundreds of thousands of our own people are jeopardizing their very existence, it is not the time to talk about the possible dangers of moderate or even considerable changes in diet. With a large number of individuals it may be of real psychological benefit to realize that they may, by personal diet restrictions, introduce an element of hazard into their lives, slight though it may be. No one could look at those vigorous young men, carrying out their college work, examinations, and physical activities in competition with their classmates, and not be impressed by the fact that the danger, if any exist, must be extremely distant.

As an index to the rather remote probability of danger one should be reminded that the modern treatment of severe diabetes is

essentially founded upon a lowering of the basal metabolism. Dr. Allen's diabetics, practically wrested from the jaws of death, present a remarkable picture. The curtailment in diet, with the low stimulus to cellular activity, has certainly in their case been a lifesaving benefit.

A research of this kind offers almost unlimited field for speculation not only in pure physiology but likewise in its practical applications to everyday life. We believe it was made with a sufficient number of men to rule out the personal equation. Indeed, the individual picture presented by each man is strikingly uniform with the general picture presented of the group. There are no exceptions.

I find myself in a novel situation as a public advocate of far-reaching dietetic alterations. Recalling my earlier objections to Professor Chittenden's inferences from his experiments, I realize that, although abstract science and propaganda are more or less incompatible, in time of stress old beliefs may well be challenged, earlier concepts discarded, and conservatism permitted to exercise a less restraining influence; hence a public avowal of change in point of view and an admission of the errors of earlier judgment are not only desirable but absolutely necessary. While still maintaining that the published records of Professor Chittenden's experiments left the desirability of a propaganda for lower protein and energy open to serious fundamental criticism, I am now convinced that his data on protein intake justified many of his public statements and recommendations. His conjectures regarding calorie needs seem in no small part substantiated by the results of this new research.

Although some of our men were under twenty-one years of age, the data obtained in our experiments have no bearing on the period of growth; the diet of the growing child should under no circumstances be reduced. Neither are the results applicable to the conditions of severe muscular work as, for example, in the army. They may, however, legitimately suggest practices for patriotic civilians not performing severe muscular work; that these standards represent the optimum needs for peace times requires further evidence for substantiation. It is quite clear that a civilian body of men could readily withstand a siege on half rations without difficulty

for several months, and since danger seems remote, that reduced rations for all adult civilians may be justifiable as a war measure for a relatively long period of months. Professor Chittenden's conclusions from his experiments that a low-protein diet is practicable seem fully substantiated; this expensive source of food material may thus be materially lowered. The calories may also, without doubt, be lowered. Indeed, it may become a serious question as to whether a patriot should be permitted in times of stress to carry excess body-weight, for the expense of carrying it around calls for calories that other people need. The excess weight is *prima facie* evidence that he is living at the highest metabolic level, higher than he needs by approximately 25 per cent., and there is no doubt that the excess weight contributes to shorten life.

Certain practical points in connection with a reduction in diet are important. Difficulties in the shape of tendency to constipation can be easily controlled by the use of bran, as was done in our study. Bran also provides a certain amount of bulk which helps materially in producing a feeling of satiety. It is quite clear that variation in diet is absolutely essential. If a person craves a certain article of food, he may eat it, but stick religiously to the "half portion." The presence of an unlimited food supply on the table makes self denial harder. Of special significance is the importance of not eating between meals and of omitting the eating of extras in the form of candy, peanuts, and minor luxuries. It has surprised us to find how large a proportion of the total diet is made up of these extras. Captain Gephart in his study of the food intake of St. Paul's School, Concord, New Hampshire, found that out of a total daily intake of 5,000 calories per boy, 647 calories were derived from extras in the form of sweet chocolate, candy, coffee buns, etc. With our control squad at Springfield when on normal diet, approximately 4,000 calories were consumed daily by each individual. Of this amount about 400 calories were obtained from extras not served at the table.

This is no time for the epicure. Every person should be under, rather than over weight and it should be popular not to be fat. Today every woman as well as man, should make it a special mission to see to the physical condition and not carry around excess

fat or live upon an abnormally high metabolic level. By this means a great saving of food in this country can be effected to the positive advantage of health. It is more than probable that with reduction in flesh, the physical appearance will be somewhat less satisfactory, for admittedly the face may appear somewhat drawn. On the other hand, it is absolutely proved that excess weight is distinctly disadvantageous to health. People especially over thirty years of age who are over weight are notoriously bad insurance risks. Even those over weights without demonstrated organic change in early or middle life show very high death rates. Nobody should be over weight; most people should be somewhat under rather than over weight. If, when the war is ended, plenty is established and the need for restriction is removed, one wishes to go back to the former metabolic level, the way is very clear. The palate will lead to this way very readily. The purse may permit indulgence but the health may really be better for a moderate reduction.

Professors Chittenden and Lusk are now in Europe with the essentials of this research in typewritten form in their hands. Certain recommendations may well be made to our Allies and, indeed, to our own non-combatants. We, who are far from the misery, trials, and torments of the battlefield, are asked to restrict our diet intake, not only qualitatively (which Mr. Hoover and his associates have so wisely educated us to do), but quantitatively. It has been a fact, and a noticeable fact, that our most intelligent and best American men and women have been eager and anxious to do all they could, even at this distance, for the sake of the great cause. In this land of plenty it is highly improbable that positive measures calling for actual caloric restrictions will have to be passed, although this is by no means an impossibility. Here, as with all conservation measures, the volunteer is the first to take action. Let no one (particularly if he be overweight) complacently say that he has done his share until some positive action for food restriction has been taken. Fortunately no special chemical analyses, no calorimetric devices, no physiological measurements are essential for the control of this factor. One has but to lower the body-weight gradually 10 per cent. and adjust the food eaten to hold it at this level. The reduction in weight should cover a period of probably two to three

months. It could be done in a considerably shorter time. When the weight is once lowered, and the calorie intake adjusted to holding the weight at that level, the patriot may feel assured that he or she is really making some positive contribution toward food conservation and making it possible to send liberally to our allies and to our own men much-needed supplies.

I cannot feel that an alteration in the army diet is justifiable at present. It is bad policy "to swap horses in the middle of the stream." The fighting unit may well be exempted from innovations but let the civilian population give this whole project a thorough, honest test, recognizing that while there may be, in certain cases, an element of hazard and in many cases an element of discomfort, the possibilities for danger in accomplishing a weight reduction of 10 per cent. are negligible. The calories thereby saved are by no means negligible, but with the sum total of our population would feed an enormous army.

II.

FOOD CONSERVATION FROM THE STANDPOINT OF THE CHEMISTRY OF NUTRITION.

By H. C. SHERMAN.

(*Read April 20, 1918.*)

Without repeating the reasons for the present program of food conservation which tends to shift the emphasis of consumption in this country toward the more perishable foods in order that a larger share of our wheat, meat, fats, and sugar may be saved for export to our army and the Allies, let us consider from the standpoint of the chemistry of nutrition whether such a change in our food habits will involve any sacrifice or rather an improvement in the average American dietary.

Recent research in nutrition puts us in position to face such problems with more confidence than would have been justified even a few years ago. Until very recently, students of the chemistry of nutrition were in the embarrassing position that rations made up by mixing in the purest forms all the substances known to be necessary never proved permanently adequate for the nourishment of experimental animals. With the discovery of food hormones or vitamins, the correlation of chemical structure and nutritive function among the proteins, and the fuller investigation of the rôle of the inorganic elements, we now believe that everything needed for normal nutrition has been apprehended and can be reckoned with, though in the case of the food hormones or vitamins the chemical identification is not yet complete.

The quantities of the various nutrients which are needed daily by the body for its normal nutrition have also been studied, with the result that each "requirement" may be stated in more or less definite quantitative terms. Thus the total food requirement (or energy requirement) in calories per man per day; the requirement

for protein, or for any individual element, in grams per man per day. The "vitamine" requirement cannot be stated in terms of actual weight either of "fat-soluble A" or of "water-soluble B," but the percentages of certain foods, rich in the one or the other or both of these dietary essentials, which suffice to make an otherwise satisfactory diet adequate for normal growth and reproduction in laboratory animals have been determined for a sufficient number of cases to enable us to take account of this factor of food value in considering the prominence which should be given to each type of food in planning an adequate and economical diet.

The quantities of nutrients required for normal nutrition as determined by laboratory experiments may be compared with the average quantities actually consumed in typical American dietaries, to find whether our ordinary food habits ensure us reasonable and proportionate margins of safety with reference to each nutritive requirement—in other words a diet well balanced from the standpoint of our present knowledge of nutrition, the older and simpler criteria of balanced diet having now been outgrown.

If in addition to such a comparison of actual nutritive requirements with the quantities of nutrients furnished in the usual food supply, we take account also of the kinds and amounts of the individual articles or types of food and the relation which each bears to the whole amount of food consumed, both as regards its cost and its contribution to each of the elements or factors of food value, we shall be able to judge with considerable confidence the nutritional significance of such a shifting of food habits as is contemplated in the program of the Federal Food Administration.

Most prominent in this program is the saving of wheat.

By people of comfortable income, wheat-saving may be accomplished by simple reduction in the amount of bread consumed. The bread thus withdrawn from the diet of the well-to-do may or may not be replaced by perishable food depending upon whether or not it is necessary or desirable to keep up the calorie value of the diet, and the weight of the body. In either case the ration with the reduced allowance of bread will usually be as well balanced as before.

But among those who must consider the cost of their food, the

attempt to reduce materially the amount of bread consumed will often be much more difficult, and to limit the poor to a per capita allowance of bread as small as that to which the wealthy can easily limit themselves would involve both hardship and injustice.

People of low income naturally and properly live more largely upon bread, because it usually furnishes more food value in proportion to its cost than any other prominent article of diet. For this reason the saving of wheat in the homes of the many can best be effected by teaching them not to eat less bread but less wheat in their bread.

Because so many of our people must for economic reasons depend so largely upon breadstuffs, it seems of the utmost importance to determine as conclusively as possible the nutritive efficiency of the chief wheat substitutes as compared with wheat itself.

A study of corn in this respect appeared particularly desirable, because it is so much the most important quantitatively of the grains which can be substituted for wheat and at the same time the one whose equal value with wheat is perhaps the most apt to be questioned, especially as regards its digestibility and the nutritive efficiency of its proteins.

In the experience of our laboratory,¹ the abrupt substitution of a large amount of corn meal for wheat flour, has sometimes, though not necessarily, been followed by slight disturbance or discomfort of digestion, but in all cases the corn protein has shown essentially the same efficiency in nutrition as has the protein of wheat. Such unfavorable effects upon appetite or digestion as were attributed to corn meal may have been due to the methods of preparing the corn products or to the fact that the diet as a whole was too bulky and too starchy for the summer weather in which the earlier of our experiments were performed.

Not only the time and temperature of cooking but also the final texture of the material may be a factor of some importance to its digestibility. The porous texture of our ordinary wheat bread favors the absorption of large quantities of saliva as the bread is

¹ The experiments with human beings here referred to were all made upon healthy adults and relate to requirements for maintenance, not for growth or reproduction.

chewed, while soft or very crumbly corn bread (or corn meal mush) may be swallowed without such thorough insalivation, and be less readily digested for this reason. By baking corn bread in thin scones it is possible to secure thorough and uniform cooking of the starch and a final product hard enough to induce thorough mastication and admixture with saliva before swallowing. Thus prepared and eaten, corn meal has in our later experiments replaced wheat flour entirely with no detriment whatever to the ease and comfort of digestion, even though the corn bread was the chief part of the diet.

Recently we have completed an experiment in which a young woman of average weight (56 kilograms), not previously accustomed to any considerable use of corn foods, has substituted such corn bread for all other bread stuffs and cereals for a month with no disturbance whatever of appetite or digestion, and has maintained nitrogen equilibrium throughout the month on a diet furnishing only 36 grams of protein daily, of which three fourths was the protein of corn meal. Practically one fourth of the total protein was furnished by milk and an insignificant amount by apple. Small amounts of sugar and of filtered butter fat were used to bring the fuel value of the diet up to the energy requirement. The subject felt excellently nourished and was ready at the first opportunity to begin a similar experiment even with the diet still further restricted by omission of the milk. During 16 days on a ration of corn meal, apple, butter-fat, and sugar, furnishing only 4.38 grams of nitrogen or 27 grams of protein (equivalent to 34 grams for a man of 70 kilograms) practically all of which was maize protein, the loss of body nitrogen was only about one half gram per day.

It is evident from these experiments that the conclusion of Karl Thomas, often quoted on Rubner's authority, which attributed a much lower value to maize protein, was erroneous. In meeting the maintenance requirements of adult human nutrition, the protein of corn meal has here shown as high an efficiency as has been reported by other investigators for wheat protein or for the average protein of ordinary mixed diet. The well-established differences of nutritive efficiency among proteins, corresponding to their differences in chemical structure, are fully recognized but are more significant for growth than for maintenance. Moreover we are here discussing

the proteins of corn as compared with wheat (not as compared with milk proteins which are certainly more efficient in nutrition). That potato protein is similarly efficient has been shown by Hindhede and by Rose and Cooper. Thus the findings of research in the chemistry of nutrition indicate that the nutritive value of the diet will be fully maintained when corn or potato is substituted for wheat. Even if such substitution results in a small diminution of the amount of protein consumed, there will still be an ample margin above the most liberal estimate of actual nutritive requirements.

Granted that corn products can be substituted for the corresponding products of wheat to any desired extent without diminution of food value as determined by carefully controlled experiments of a month's duration, the question may still arise whether the results would be equally favorable in case the substitution of corn for wheat were continued much longer and in the case of growing as well as full-grown persons. This question cannot well be answered directly by experiments upon human beings—if for no other reason than that a research cannot be prolonged indefinitely and still be completed in time to be of use in connection with the present emergency work of food conservation. But an adequate answer appears to be furnished by the investigations of McCollum in which laboratory animals (chiefly rats) have been kept on experimental diets of wheat or corn with the necessary supplements often for their lifetime and in many cases for more than one generation. Such experiments should bring to light any differences which might be conceived to exist in the most elusive factors of food value or in the general wholesomeness of the two grains. In recent summaries of the results of such research, McCollum has repeatedly stated that wheat and maize are essentially alike in their dietary properties. If this seems surprising in view of the well-known inadequacy of zein when fed as the sole protein of the diet, it should be recalled that Osborne and Mendel, to whom the knowledge and explanation of this deficiency of zein is so largely due, have also shown that the other chief protein of corn, maize glutelin, is adequate to meet all protein requirements and to maintain a normal rate of growth in the young. They have also shown beautifully that zein, while inadequate alone, may yet take the major part in meet-

ing the protein requirements, either of maintenance or of growth, when it is supplemented by even a small amount of milk protein.

That the supplementing of the grain protein by milk is of greater importance during growth than in the mere maintenance of a full-grown person is fairly obvious from the fact that in the latter case it is only necessary to maintain an already established equilibrium between tissue protein and amino acids. *Any* of the amino acids whose radicals are contained in tissue proteins may be expected to function in such maintenance, whereas there can be no growth unless *all* the amino acids represented in tissue proteins and not formed in the body are present in sufficient abundance.

Even in the case of the full-grown organism persistent use of a diet consisting *too exclusively* of grain products, or seeds of any kind, may lead to unfavorable results, but this is true of wheat as well as corn and is no objection to the substitution of the one for the other.

Such substitution of corn (and presumably of other grains) for wheat will leave practically unchanged the nutritional efficiency of the diet and the usual margin of safety above actual requirements which is characteristic of the average American food supply.

What then is this margin in the case of the different factors of food value and how will it be affected by the other substitutions which the present food situation demands?

In view of the findings just presented by Dr. Benedict and the fact that in most food studies outside of the laboratory it is not practicable to make accurate record of the muscular activities of the persons concerned, any attempt to estimate the percentage by which the total food intake of the average American family exceeds its actual food requirement as expressed in calories, would necessarily involve several assumptions the discussion of which would extend the present paper beyond its assigned limits.

In the study of protein requirement the assumptions are fewer because muscular activity is here not an appreciable factor, but the data of different investigations are less concordant than in the study of energy metabolism. The results of a review of the literature of protein requirement up to 1917 with an attempt to select the experimental data which are comparable with each other and applicable

to the problem of the amount of protein actually needed for normal human nutrition have recently been discussed elsewhere.² The average of the "requirements" indicated in the 86 experiments which seemed to be applicable under the necessarily somewhat arbitrary criteria adopted for the sake of minimizing the personal equation in selection and interpretation of results, was 49.2 grams (or say 50 grams) per man per day, which agrees almost exactly with Chittenden's estimate based chiefly upon the results of his own experiments. Thus the net result of all subsequent work up to date does not differ materially from Chittenden's findings of a decade ago. This may be accepted as the best evidence yet available regarding the amount of protein actually required in normal human nutrition without entering upon any discussion of the question as to how much more than this it is desirable to consume. In other words in speaking of the requirement we imply nothing as to the best dietary standard for protein.

As compared with this actual requirement of not over 50 grams, the average amount of protein in typical American diets, as judged from the 250 studies of families or larger groups the data of whose food consumption has been most fully worked out, is 106 grams per man per day. The average of typical American diets thus shows in its protein content a margin of safety of 112 per cent.

Of the inorganic elements essential to nutrition, most are believed to be furnished in abundance by the ordinary American food supply with the table salt commonly added to it, but recent research has shown that three of these elements cannot properly be dismissed with this assumption. These are phosphorus, calcium, and iron.

It is sometimes stated that our knowledge of the amounts of these elements required in nutrition is so meager as to make the interpretation of dietary data more difficult here than in the case of protein. Until recently this was true of all three of these elements and it is still true of iron; but the quantitative metabolism of phosphorus and calcium has lately been investigated with sufficient thoroughness so that we now know the normal nutritive requirement for these elements with about the same degree of accuracy as we know the protein requirement and can estimate the margin of safety

² Lecture before the Harvey Society, New York, Jan. 12, 1918.

in the average dietary and the likelihood of deficiency in individual cases as well for phosphorus and for calcium as for protein.

The phosphorus "requirement" as indicated by the results of 87 experiments averages 0.88 gram per man per day,⁸ and the average amount in 250 American dietaries was 1.60 grams, a margin of 82 per cent.

The calcium "requirement" indicated by 63 experiments averages 0.45 gram,⁸ and the average amount in typical American dietaries was 0.74 gram, a margin of 64 per cent.

It will be seen that the margin of average consumption above the bare requirement is less for phosphorus than for protein, and narrowest in the case of calcium. Actual deficiencies in the sense of a rate of consumption below the average of the bare requirements for normal maintenance, are exceedingly rare in the case of protein, not so rare in the case of phosphorus, much more frequent in the case of calcium. It appears that the American dietary is more often deficient in calcium than in any other chemical element whose metabolism has been studied.

Probably because of the ability to transfer calcium from the bones to the soft tissues, the body may continue to lose this element for a long time as Forbes and Beegle have shown strikingly in the case of milch cows. But it does not follow that the loss of body calcium is to be regarded with indifference. Mendel has written regarding his recent experiments that "animals may be in excellent nutritive condition in so far as protein is concerned for long periods of time while they are still losing calcium from their bones. It then happens that suddenly a collapse comes for which there is frequently no obvious explanation." And McCollum has found in his studies of laboratory animals that it is largely because of insufficient calcium that such animals do not show normal nutrition when kept continuously upon rations consisting too exclusively of seeds. Our investigations based chiefly upon the chemical analysis of the entire intake and output of the human organism, while quite different in method, have led to the same view regarding the importance of calcium as has been reached by Mendel and by McCollum.

⁸ These phosphorus and calcium "requirements" are derived in the same manner as the protein "requirement" of 50 grams per man per day explained above.

American dietaries, both urban and rural, are more likely to be deficient in calcium than in any other individual element because they tend to consist too largely of the products of seeds together with meats, fats, and sugar with too small a proportion of milk and vegetables.

All meats are very poor in calcium; purified fats and sugar are practically devoid of it. On the other hand milk, eggs and green vegetables are rich in calcium; other vegetables and fruits contain it in fairly liberal amounts. Hence decreased consumption of meats, fats and sugar, with increased use of milk, eggs, vegetables and fruit will constitute an important improvement in the typical American dietary.

Detailed study of the data of the 250 typical American dietaries already mentioned shows plainly that as the relative expenditure for meats, fats, and sugar decreases and that for perishable foods increases the dietaries become more adequate and better balanced as regards the various factors of food value which can be expressed in quantitative terms—energy value, protein content, and amounts and proportions of the various ash constituents or inorganic elements.

So far as calcium and the other inorganic elements are themselves concerned, they might be supplied in the form of simple mineral substances such as calcium phosphate, but in human dietetics it is more feasible to teach the use of familiar than of unfamiliar articles, and by the use of sufficient milk and vegetables to provide a liberal supply of calcium the diet is improved in other respects as well.

The larger use of such perishable foods as milk, vegetables and fruit is beneficial in several directions which as yet are not susceptible of quantitative measurement—such properties as the promotion of growth, and the prevention of neuritis, scurvy and pellagra, whether the latter be strictly nutritional diseases or not. Such benefits are probably due in part to the unidentified essential substances “fat-soluble A” and “water-soluble B” both of which occur abundantly in milk, eggs and many vegetables, and in part to those chemical and physical properties of fruit, vegetables and milk which are favorable to intestinal hygiene and so protect the body from objectionable products of intestinal putrefaction.

It has long been known but perhaps never sufficiently emphasized that the milch cow returns for human consumption a much larger proportion of the food value of what she eats than does the animal which is raised for slaughter. This is strikingly true not only of the previously recognized factors of food value but also, and apparently to an even larger extent, of the so-called vitamins. These are contained in abundance in green leaf fodders such as grass and hay. The vitamins thus consumed are stored in the animal tissues to only a limited extent, but are transferred in relative abundance to the milk. Thus the vitamins of coarse materials not directly available as human food are brought into form for man's use, very efficiently through milk production, very inefficiently through the production of meat. Not only is milk the most economical intrinsically of the animal foods of farm origin, but of even greater interest is the positive demonstration by fully controlled experiments like those of Osborne and Mendel and of McCollum, that a liberal use of milk in the diet is the best safeguard against any deficiency which might possibly arise through restricted choice of foods and the safest way to ensure that the consumption of enough food to supply the energy needed shall meet all other requirements of nutrition as well.

Thus in bringing a larger share of our corn crop directly into human consumption and in giving to such perishable foods as milk, vegetables and fruit a more prominent place in the diet, we shall be working toward permanent improvements in our national food economy at the same time that we save the wheat, meat, fats and sugar which are needed for our armies and the Allies.

LABORATORY OF FOOD CHEMISTRY,
COLUMBIA UNIVERSITY,
April, 1918.

III.

SOME ECONOMIC ASPECTS OF THE AMERICAN FOOD SUPPLY.

By J. RUSSELL SMITH, PH.D.

(Read April 20, 1918.)

We are at last planning for a long war. Munitions that cannot be ready until the spring of 1920 have been ordered. The food supply and its control by government also need to be put on a permanent, a scientific, and a reorganized basis.

The United States has great food possibilities as follows:

1. We have enormous resources of unused land in villages, towns, suburbs, cities, and on farms and in land yet unreclaimed.
2. We have enormous resources of labor now represented by leisure, by sport, and by industries which are dispensable if winning the war is our prime object. These industries might therefore divert labor to food production if we should become convinced that an emergency exists.
3. We have an enormously strong position in that at present our agriculture has an animal base, namely, that most of the proceeds of the American farms and fields go to feed beasts. Much of it can be diverted to men if the need arises.

We should not take too much comfort from these descriptions of food resources. They may have the same significance for an army, hungry to-day, that our twenty million young or youngish men have for an army hard pressed to-day. Both require months or years to become effective. The food resources call for energy and intelligence if they meet the need. Unfortunately, the process of putting energy and intelligence into the food question must face the troubles that arise from democracy. In America everybody can howl. Every man and some women can vote, every interest can lobby and hire advertising. It can also have friends if not tools in authority. These

forces that sway government arise from a citizenship of whom the great mass are economic illiterates. This is unfortunate, for government is becoming more and more the application of economics, especially in war time, and we as yet have very inefficient reasons of determining whether those placed in supreme authority have economic knowledge.

Our chief task with regard to food is to save ourselves from our beasts; namely, to shift agriculture from the production of food for animals over to the production of food for men. Agriculture, like the other industries, responding to the law of supply and demand, had slowly adjusted itself to a condition of world trade which, as we well know, has been suddenly destroyed in such a way as to throw upon us greatly increased demands for both bread and meat, but especially for bread. This means that we must either increase our total production or shift our production from one class of goods to another. It is very doubtful if we can hope for a total increase in agricultural products, in consideration of the fact that hundreds of thousands of people have recently left farm labor for the more attractive prices of munition plants and other city opportunities, and other hundreds of thousands are going off to the army.

Therefore, we must reduce something. What shall be reduced? Since the main products of American farms may be classified ultimately as fruits and vegetables, bread stuffs, dairy products, meats, and fibers, we must look over the list carefully and see where we can shorten up. Examination of the facts will show that there is but one place. We must have fibers for clothing. We must continue to have bread, more of it rather than less, much more indeed. We must continue to have fruits and vegetables, more of them rather than less. We should not attempt to reduce dairy products. It is upon meat and meat alone that we have the possibility of shrinking. The beasts, the blessed beasts, by their deaths, can save us. Their bodies, if used for food, fill our plates once. The grain they would have eaten had they lived will fill our plates several times over.

It is difficult to overestimate the importance of the fact that American agriculture has an animal base. In China, Japan, and parts of India, animals are only one-twentieth part as numerous in proportion to population as they are here. There man raises food

by hand labor and eats it himself. If he misses a crop, there is famine, which in those regions has killed more people in the last hundred years than even this terrible war has killed. In this country we raise a crop, feed most of it to the beasts. If we have a shortage, we kill a few of the beasts and eat them and a part of their food. Fortunately our animals are in the habit of eating largely of food that we can eat, in which respect our agriculture differs greatly from the agriculture of certain other peoples. For example, the Arab of the desert has a great wealth of beasts, but his camels, goats, sheep, and donkeys eat grass, coarse herbs, and bushes which he cannot eat; whereas, our animals are grain eaters to the extent of three to four billions of bushels a year. Therefore our problem is greatly simplified by this precious element of elasticity.

When we start out to shorten our animal supply we cannot do it, however, in an indiscriminate way. The horses and mules we must have to maintain production and keep the army going. We must have the cows for dairy products. We must have the sheep for wool and also mutton. We must keep the hens for their invaluable eggs. There remain but two classes under consideration for the possible shrinkage; namely, swine and beef cattle. As between these two we have the fact that swine are much more efficient in that they return 29.9 per cent. of the production value of the food eaten, while the steer returns but 14.8 per cent.¹ Therefore it is plain that the simplest place to gain bread at the expense of meat is to reduce our holdings of beef cattle not only for the reason of their inefficiency as meat producers when the food they have consumed is considered, but also because the food eaten by beef cattle can be taken over by the more valuable animals, especially in this particular emergency; namely, the cow, the horse, the mule, the sheep, and even the goat.

It is a misfortune of society that attempts to change any industry

¹ Eckles and Warren, "Dairy Farming," p. 8.

On the basis of the grain eaten by these animals—"It may be roughly estimated that about 24 per cent. of the energy of grain is recovered for human consumption in pork, about 18 per cent. in milk and only about 3.5 per cent. in beef and mutton. In other words, the farmer who feeds bread grains to his stock is burning up 75 to 97 per cent. of them in order to produce for us a small residue of roast pig (he should have said meat) and so is diminishing the total stock of human food."—"Roast Pig," *Science*, 1917, XLVI., 160.

whatsoever are bound to affect some citizen's profits. The most fervid oration I have heard since the war began was a cattle dealer decrying meatless days, and so far as I know Uncle Sam has done nothing to shift the emphasis of meat production except to exhort, and some of his exhortations have been strictly pro-German. Many efforts, unofficial and perhaps even official, have been directed toward the positively inefficient line of trying to increase beef cattle instead of urging that the male calf should be hustled off to the shambles as quickly as possible to make room for his betters.

Specifically the food tasks of the government, aside from rationing, have been and will be chiefly three: (1) to increase production of meats and fats and to reduce their consumption; (2) to conserve the supplies on hand, particularly bread stuffs; (3) to increase production of bread stuffs and substitutes. In this work the administration during the first year has had to face very great difficulties—for the first months an entire lack of formal organization and the absence of adequate legislation. In Congress and out, the friends of Germany, the friends of the profiteer, the foes of change, and those still asleep have fought the rationalizing of our food administration and have tried to baffle and hamstring it with meager powers. Throughout its career the Food Administration has had to combat pro-Germanism of some people, a lack of patriotism of others, an universal love of what we are used to eating, our ignorance of the real situation and our continued action under the feeling that the war was still 3,900 miles away, and finally the difficulties of trade readjustment and industrial readjustment where changes have been attempted.

There is every reason to believe that in the future the government will have a different intellectual background because of a stirring, a conviction that is resulting from the terrible battles now in progress, and from the fact that we are actually at least participating in the war itself, though even yet to a very small extent.

What changes in food matters do we need as we become increasingly resolved to apply ourselves and our resources to the war?

I. Increasing the Supply and Reducing the Consumption of Meats and Fats.—The government's general policy of letting meat prices alone is excellent. Excellent also is its policy of standardizing

profits of packing companies and checking their profiteering. The meat supply has thus had the high price stimulus to production and the high price check to consumption. Excellent also, probably, was the first compulsory increase of agricultural production: namely, the prohibition of the sale of hens until the first of May (later amended to April 20), although with the high prices of grain it has probably resulted in losses to a number of poultry keepers, and they may not get caught in that trap again.

The widespread campaign conducted by many newspapers last year about not killing the calf has, as above mentioned, been a positive injury to the country, in so far as it has resulted in the production of the least efficient of our meat producers. "Kill the bull calf and buy a sow," would have been a far wiser motto. Instead of urging the production of beef cattle, there should be as a war measure an annual tax of \$10 or \$15 a year on every steer for every year of his life. Pigs, sheep, and goats should be encouraged. Eating of horse meat should also be encouraged, and as soon as possible provision should be made to bring 15,000 or 20,000 fine fat whales per year from Antarctica, where they have now and for decades been wasted. Fortunately the experience of many nations shows that we can get along nicely with half our meat consumption if we have to.

II. *Food Conservation.*—Real food conservation is rationing. The other methods are small imitations. There has been a splendid educational campaign conducted urging us to spare the wheat, the meat, the fats, the sugar. To it I have willingly and gladly given many days of hard labor without pay. The campaign was a necessity, but I do not believe that so long as conserving remained on a voluntary basis, it can be shown to have been accompanied by any net saving of food. The intelligent, who because of that fact are nearly always patriotic, have stinted themselves. The great majority, who are not intelligent, have, because of high war wages, been able to indulge themselves. Undoubtedly if the facts were all in hand, we should see the same thing here as was found in England where a similar campaign and similar rise in wages was accompanied by actual increase in consumption of staple foods in the early period of the war. The campaign for voluntary rationing had its

real results in the education of the people of a democracy so that they would stand for the necessities of compulsory rationing when it came. It has now come, and it will go sometime after the end of the war, probably not before.

The actual food saving results for the first months, are, I fear, too nearly indicated by the action of a certain railroad which in April of this year on its dining car bill of fare flamboyantly advertised itself as cooperating with the United States Food Administration, announced that luncheon was a wheatless meal, and then a few lines below offered for luncheon the following:

Rye bread and butter, 10 cents.

Graham bread and butter, 10 cents.

Boston brown bread, 15 cents.

Dry or buttered toast, rye or graham, 15 cents.

Virginia corn muffins, 10 cents.

Mashed potatoes, 20 cents.

It refused to sell to any person a second order of Virginia corn muffins, and meanwhile charged 20 cents for a portion of mashed potatoes, when it is well known that the potato is the most important substitute for wheat and its near equals rye and barley. Furthermore, potatoes were at that moment a drug on the market, as the Food Administration had announced. If that railroad had been scientifically trying to help the Food Administration save wheat rather than indulging in some pious self-advertising, it would have sold mashed potatoes for 5 cents or at most 10 cents, and corn bread for 10 cents, allowing a repeat order, and charged 20 cents or 25 cents for wheat or rye bread, thereby automatically reducing the amount sold to a fraction of actual sales. Similar examples could be adduced indefinitely.

It has also been a great misfortune that the people have been unable to secure adequate quantities of substitute cereals at reasonable prices. A week ago to-day corn flour was quoted to me, four blocks from here, at 10 cents a pound, and wheat flour at 8 cents a pound. This indicates a deplorable condition in a country short of wheat and actually producing more than three times as much corn as wheat, and with a government that has begun to substitute statute law for the law of supply and demand.

III. *Increasing Production of Bread Stuff and Bread Substitutes.*—In the increasing of food production, the first year of the democracy at war and apparently even the second year promise to demonstrate democracy's weak point rather than its strong point. If anything is plain it is that we need an increase of food supplies, particularly bread. Yet that part of the democracy that can make itself most felt in newspapers, in elections, in congressional lobbies, is the city consumer, and one of the first acts of government with regard to the bread supply was to interfere with the law of supply and demand by guaranteeing increased home consumption and reduced home production. Despite innumerable reports that maximum price-fixing had been unsatisfactory in Europe, we tried it. As one of the first big steps in the United States we reduced the maximum price of wheat at a time when more wheat was needed. We also fixed a minimum price for the 1918 crop lower by a dollar than the price prevailing in the spring of 1917. The American farmer quietly but effectively made his answer. The government, through the Department of Agriculture, called for planting of 47,337,000 acres of winter wheat, and it got 11 per cent. less than this, or 42,170,000, almost exactly the amount sown in 1914.

Probably the worst part of this wheat price fixing is that it resulted in a destructive price ratio. The high prices of meat pushed the price of corn to such a figure that in many parts of the country it was cheaper to feed the pigs on wheat and rye than on corn, and you may depend upon it many of these four-footed brethren got the breadstuff. In some part of New York state wheat was 40 to 50 cents a bushel cheaper than corn. The production of such a condition by legislation as our Congress brought about, is not to be called food conservation. It is food destruction. As an outraged citizen I protest against legislation that makes me eat corn and makes the pig eat wheat. If I were a pro-German I would secretly applaud it.

What of the future? What steps has our government taken to guarantee an abundant supply of bread and bread substitutes? We are sitting with undue serenity behind the hope of a "normal average production." To quote the exact words of a spokesman of the federal government, "What the world needs from the United States in order to get through comfortably next year is 850,000,000

bushels of wheat. An acreage sufficient to produce even more than this crop, *if we have a normal average production*, has been and is being planted." This I assert is a positive menace. While I am not conversant with the plans of the German high command, I do not for a moment believe they have gone into this war leaving any vital point so exposed as to be dependent upon "a normal average production," if there is any way of avoiding it. We have abundant ways of giving further guarantees of bread substitutes, and we have not done so.

In engineering there is a practice of giving a wide margin of safety in building. A structure is made five or ten times as strong as the normal average load it is to carry. The peril that lies in this dependence upon a normal average production of wheat is shown by an examination of the irregularities of production in our regions of surplus. More than any other important crop regions in the United States our regions of wheat surplus are bounded by the perilous bounds of drought or frost. The western limit of the wheat border in Kansas is a drought line. The same is true in Nebraska, in South Dakota, in North Dakota. The same thing is true along the whole wide sweep of the southern edge of the West Canada wheat country, while its northern edge is limited by the uncertainties of cold waves and of frost. These unpredictable perils explain how Canada has been able to produce in 1914, 161 million bushels, in 1915, 376 million bushels, and in 1916, 220 million bushels—a fluctuation of more than 100 per cent. We have shown ourselves capable of fluctuations within twelve months from 1,025 million bushels in 1915, to 639 million bushels in 1916, and we were unable to raise the amount substantially in 1917 (651 million bushels). Except as a last refuge of the hard pressed we have no right to depend upon "normal average production" when Minnesota has shown herself able to vary her annual yield per acre from 17.0 to 7.4 bushels; North Dakota from 18.2 to 5.5; South Dakota from 17.1 to 6.8, all within the short gap of the same twelve months.

In the same limit of time Kansas has jumped within recent years from 10.7 to 20.5 bushels per acre. In one season Nebraska has plowed up 75 per cent. of her winter wheat because it was not worth keeping.

How can we guarantee the bread supply? There is of course always corn, which we do not like, and which we have never yet eaten very heavily. The real substitute established in our kitchen habits is the potato, and it is running straight toward ruin, if we depend only upon normal average production. The potato is the real substitute for bread in the American dietary. Properly dried it can be quickly made into much more of a substitute, as has long been the case in Germany. Professor Laughlin states in his recent book on war credit that in the food of the United States the potato is half as important as wheat and rye combined. In France it is an equal of both grains, while in Germany the potato is three to four times as important as these two bread stuffs. Germany has a real potato industry on an industrial basis. Ours is based on a gamble. A bulletin of the United States Department of Agriculture shows that the German potato supply is guaranteed at an amount far above needs for human food because of industrial uses such as alcohol, starch, stock food. These things have a fairly constant price, so the Germans have all the potatoes they want at a price which has fluctuated only 27 cents in a period of five years. Chicago meanwhile had a price fluctuation of \$1.34 per bushel. It is on the potato that Germany has thus far won her campaigns. Without it she would have perished any year. Our potato is a peril because it is a gamble. We have not developed a stable outlet for a surplus crop such as is afforded by the German starch, alcohol, flour, and forage products. Accordingly if we have a slight surplus they are thrown away, the market is glutted, as at the present moment, and the farmer is discouraged. The next year (as at the present moment) he plants a light crop and that potato season ends in shortage with high prices to stimulate the farmer to plant a large crop, and so on. The cycle has run with little variation for thirty years. Last year we had an excellent demonstration of the scanty end of it. This year even in our flour shortage we have an excellent demonstration of the glut end of it. Next year, unless there is a failure in all the signs of the past, aggravated by the conditions of the war, we are sailing straight into a potato shortage and also the possibility of a flour shortage. And the government is doing nothing about the potato question.

For a year we have needed a potato high minimum guaranteed

price just as we have for wheat, for exactly the same reason, so that we might shift the energies of our farmers from producing steer food to producing man food. It would take a very small shift, for our corn acreage in 1916 was 106 million acres, our wheat 53 million acres, and our potato area was 3.5 million acres—an insignificant proportion, perhaps 3 or 4 per cent. of our possible potato land, but enough under ordinary conditions to glut the market about every other year. Next spring it should be oversupplied again, and the government should guarantee it in advance and be prepared to conserve the potatoes by drying them.

The labor supply is a very important part of food production. Washington reports that 100,000 men per month are now going into war industries. The draft is taking them faster than that. Munitions and luxuries can both pay more than the farmer can. This is perilous business. With increased food demands and a government that is tinkering with the law of supply and demand, food shortage may catch us before we know it. The government should make some application of prophecy to the nation's needs and tendencies, and fill the most important needs before it is too late. Food disaster is a real disaster.

The government that rules us in the near future, will be a government well informed, and having the courage of its convictions. The last point will have much to do with deciding what language it speaks. Let us hope that the U. S. government of 1917, with its frittering of human energy, is gone. Last spring when Congress was discussing selective draft, college faculties urged students to leave their classes and go to the farm. Through my own personal office I cleared 418 University of Pennsylvania students for the farm, within five weeks after the declaration of war. This winter I have had the humiliation of seeing the food consumed by the makers of chewing gum, high-heeled shoes, limousines, and other products which thus are made to rank as of more importance than education.

The government is now formally asking, through the Department of Labor, for boys to leave school and go to farm work. It is an excellent principle, the selective draft idea applied to human time. Drop your books and take up the hoe. But what about the high-

heeled shoe, the limousine, and the gum—should they outrank both education and food? It would seem that at the present moment they do, for officially the government has called for the college student and not for the gum maker.

We have an extensive reserve of skilled agricultural labor, the many, many thousands of farmers' sons and farm hands who have gone forth from the farm and who will go back, temporarily at least, if the pay is good enough.

Labor cannot be drafted in the United States as easily as a soldier can be drafted. It can be inspired some, and for a safe dependence it can be paid. That is the practice in producing munitions and clothes. Food production is no exception.

In conclusion and summary, the proper utilization of our food resources during this war requires at the hand of government:

1. Price regulation to stop undue profiteering.
2. Price guaranteeing of bread and bread substitutes at such figures and such relative figures as to assure an abundant supply of the same at the expense of beef and other meat if necessary, but not at the expense of dairy products.
3. Material aid (other than talk) in the manufacture and distribution at reasonable prices of wheat substitutes if it is necessary for the people to use them.
4. Creation of new labor supply for the farm, by
 - a. Young men under draft age,
 - b. Women,
 - c. Workers drawn from less vital industries.
5. Deportation of all idlers, whether they use an old tomato can or 12 cylinders.
6. The building up as soon as possible of a war pantry of surplus breadstuffs of at least 200,000 bushels.
7. Development of local supplies wherever conditions are favorable. Thus war gardens, canning clubs, drying clubs, curb markets, local storages, etc., will do much to simplify the railroad burden.
8. Drastic simplification of distribution by eliminating waste motion of which we now have an almost unbelievable amount.

9. We need to have these things done as England manages her commerce, by a board of competent experts free to administer a law with sweeping powers. As it is now, it is done by elective congressmen not always above the suspicion of economic illiteracy and of representing a district rather than the United States. Congress is no more capable of setting the price of wheat by statute than it is of fixing a railroad rate. The Interstate Commerce Commission and the War Industries Board are good examples for Congress in the conduct of our food policy.

WHARTON SCHOOL OF FINANCE AND COMMERCE,
UNIVERSITY OF PENNSYLVANIA,
April, 1918.

ON THE NUMBER OF SPIRAL NEBULÆ.

By HEBER D. CURTIS.

(Read April 20, 1918.)

The probable total number of the spiral nebulæ is a matter of considerable importance in all theories bearing on the constitution of these objects and their place in the sidereal plan. Prior to the introduction of photographic methods fewer than ten thousand nebulæ were known. One of the first results deduced by Director Keeler from the program of nebular photography, which he inaugurated with the Crossley Reflector, was that there exist many thousand very small, uncatalogued nebulæ, the great majority of which are undoubtedly spirals. Early in the course of this program, and before photographs of many regions were available, he estimated that there were at least 120,000 small spirals, and regarded this estimate as a very conservative one.¹ On completing the original Keeler program Perrine² came to the conclusion, from counts of small nebulæ made on fifty-seven of the one hundred and four regions of that program, that at least 500,000 small nebulæ were within reach of the Crossley reflector, and deemed it not improbable that the total might ultimately exceed 1,000,000. Later, Fath,³ working with the 60-inch Reflector at Mt. Wilson, took a series of 139 plates at the centers of the Kapteyn areas, on which 1,031 nebulæ were recorded, and estimated that the number within reach of the 60-inch Reflector with exposures of one hour on Lumière Sigma plates (an approximate equivalent to the exposures of the Crossley program) was 162,000.

The great numbers of small spirals found on nearly all plates of regions distant from the Milky Way long since led me to the belief that Perrine's estimate of half a million was likely to be under,

¹ *Ap. Jour.*, 11, 325, 1900, and *Publ. Lick Obs.*, 8.

² *Lick Obs. Bull.*, 3, 47, 1904.

³ *Astr. Jour.*, 28, 75, 1913.

rather than in excess of, the truth. The extent of the existing photographic material now makes possible and useful a new determination of the number of the spiral nebulæ. Descriptions of 762 nebulæ and clusters are being published in a University of California semi-centennial volume, and, in preparing this paper, I have made counts of the numbers of small nebulæ occurring on all the available regions of the complete Crossley program covered by the above list, extending from 1898, when systematic work was commenced at Mt. Hamilton with this instrument, to February 1, 1918.

In all, 439 regions were available for these counts, giving a total of 5,698 small, uncatalogued nebulæ. To these must be added the 513 spirals described in the list, making the total number of all nebulæ found in all the regions 6,211. In the belief that practically all these small nebulæ are spirals, I have designedly omitted the diffuse nebulosities and the planetaries.

The exposed area of a Crossley plate is about nine tenths of a square degree; the edges and corners of this area are, however, so poorly defined, owing to the distance from the optical axis, that only the brighter of the small nebulæ can be picked up in these outer parts of the plate. The greater proportion of the small nebulæ are found in the more central parts having an area of six tenths of a square degree, or less. I have assumed 0.75 of a square degree as the average effective area on which the counts were made; this is certainly somewhat in excess, but is an error on the conservative side.

We shall first assume that these 439 regions are sufficiently uniform in their distribution to be taken as a fair representation of the whole sky; their area will be 329.25 square degrees. If the proportion shown by these regions holds over the entire sky, we should expect the number of the spiral nebulæ to be 778,000. A plot of the regions shows that their distribution may well be regarded as an approximately uniform one. There is, it is true, a marked concentration of regions in the vicinity of the north galactic pole, but this would appear to be balanced by a similar preponderance of regions in the Milky Way between 17 and 20 hours of right ascension (see Fig. 1). If we divide the celestial sphere into two equal areas, one consisting of a zone 60° wide extending for 30° on each side of the galactic plane, and the other comprising the two zones of 60° radius

about the two galactic poles, we shall find that 217 regions, or 49.4 per cent., are located in the first, or galactic area, and 222 regions, or 50.6 per cent., in the polar areas. The balance in the distribution of the regions in the galactic and extra-galactic zones is, then, nearly perfect.

On the other hand, bearing in mind the well-known concentration of the spiral nebulæ in the vicinity of the north galactic pole, and

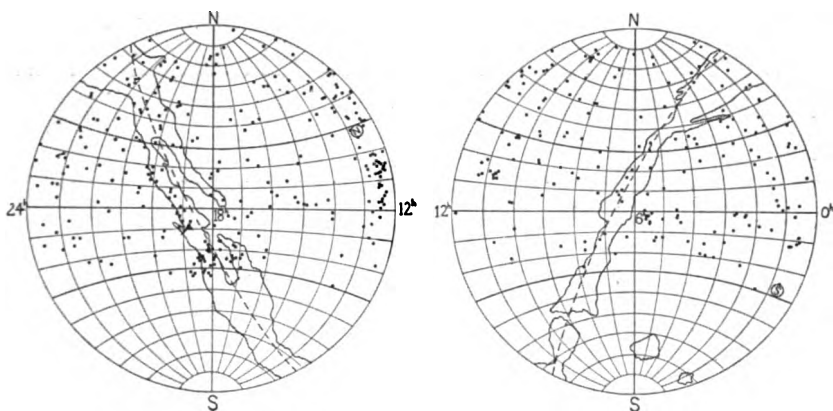


FIG. 1. Chart showing distribution of regions on which small nebulae were counted.

the fact that the present program deals primarily with the regions containing spirals, it is necessary to investigate further any possible effect which a concentration of regions near the north galactic pole might have upon the resulting estimate. This objection was urged by Fath (*loc. cit.*) in explanation of the difference between his estimate of 162,000 and the 500,000 of Perrine. He found, on plotting Perrine's regions, that 33 per cent. of these were within 45° of the north galactic pole, while less than 20 per cent. of the Kapteyn areas were within this distance. In the present program I find that 117 regions, or 26 per cent. of the regions which I have used, are situated within 45° of the north galactic pole, in an area amounting to but 14.6 per cent. of the sky, and these 117 regions contain 2,997 spirals, or about 48 per cent. of the whole.

To avoid the effect of this concentration in the north polar galactic area, it will be advisable to subdivide the material available. We

may divide the celestial sphere into four areas, two of which will be the zones of 45° radius about the two galactic poles; a third area will comprise the two zones, each 15° in width, extending from -30° to -45° and from $+30^\circ$ to $+45^\circ$ galactic latitude, and the fourth will be the zone 60° wide extending from -30° to $+30^\circ$ galactic latitude. The results are indicated in the following short table:

Galactic Latitude.	No. Regions.	Sq. Deg.	No. Spirals.	No. per Sq. Deg.	No. in Area.
$+45^\circ$ to $+90^\circ$	117	88.50	2,997	34	205,000
-45° to -90°	43	32.25	918	28	169,000
$\pm 30^\circ$ to $\pm 45^\circ$	62	46.50	1,117	24	204,000
-30° to $+30^\circ$	217	162.75	1,179	7	144,000
Totals.....	439		6,211		722,000

It will be seen from the above that there is a concentration of the smaller nebulæ in the vicinity of the north galactic pole similar to that which obtains among the larger, visually discovered, spirals, and that the density about the south galactic pole is somewhat less marked. The data given in the third line of the table are of special interest, showing that the small spirals persist to a distance of at least 60° from the galactic poles, with only a slight diminution in the degree of density which obtains in the polar areas.

As this revised estimate, 722,000, is equal to that of Fath plus that of Perrine, with several thousand to spare, a discussion of the possible reasons for the discrepancy becomes imperative. The following points may be considered:

A. It may be urged that my count has not been sufficiently conservative, and that I have possibly included many spurious objects. The detection of the faintest and smallest nebulæ is very largely a matter of experience, and all who have worked with photographic plates soon learn, by hard necessity, to recognize the average flaw at a glance. A very large proportion of the objects are unmistakably nebulæ. As to the faintest nebulæ, it is astonishing how faint and small are the nebulæ which two "clean" duplicate plates will reproduce. For a large proportion of my regions no duplicate plates exist, and I have been necessarily guided by the experience derived

from regions taken in duplicate. I am unwilling at present to admit that as many as five per cent. of the nebulæ counted by me are spurious. Even if twenty per cent. were spurious, we should still have to account for over half a million nebulæ.

B. The theory may be advanced that the small spirals occur in greatest profusion in the regions contiguous to the larger members of the class, which might explain why fewer nebulæ were found by Fath. His plates were taken at the centers of the Kapteyn areas where the larger nebulæ would be included only by chance, whereas, from the purpose of the Crossley nebular program, nearly all the plates have some N. G. C. object central. This point is difficult to prove or disprove without a special investigation comprising many plates taken at random in the galactic north polar region. It is certain that the small spirals frequently show a gregarious tendency; sometimes one half of a plate will record many small spirals while the other half records very few. The greatest number of nebulæ found on a single plate was 304 (checked by a duplicate plate) in the region of $12^{\text{h}} 55^{\text{m}}, +28^{\circ} 30'$ (shown in Fig. 2); the region about N. G. C. 4826, less than 7° distant from this, shows but 2. While the small nebulæ are evidently quite irregular in their distribution, it would seem that the large number of regions included in this discussion is sufficient to afford a true representation of their average frequency.

C. Sharp focus and perfect images are essential for the detection of the smallest and faintest spirals. On plates where large numbers of small nebulæ are found, the majority are, as a rule, detected in the area $20'$ in radius about the optical axis as center, comprising only 0.35 of a square degree. At a distance of $30'$ from the optical axis the parabolic images are very poor, and only the brighter of the small nebulæ can be detected in these regions, the faintest nebulæ being obliterated by the blurring and spreading of the image. Dr. Fath used very large plates, $6\frac{1}{2} \times 8\frac{1}{2}$ inches in size, in his work on the number of the small nebulæ, with the 60-inch reflector, and it appears that he used almost this full area, inasmuch as he states that the used area of his plates was 1.88 square degrees. As the full area of the Crossley plate is 0.9 square degrees (and the outer portions of this are so poor because of the parabolic distortions that

the effective area used in my counts is believed to be less than 0.75 square degrees) this would mean, if the two reflectors were of the same focal length, that the images on one half of the angular area of the large plates used by Fath were worse than those in the rejected edge strips of the Crossley plates. But the greater focal

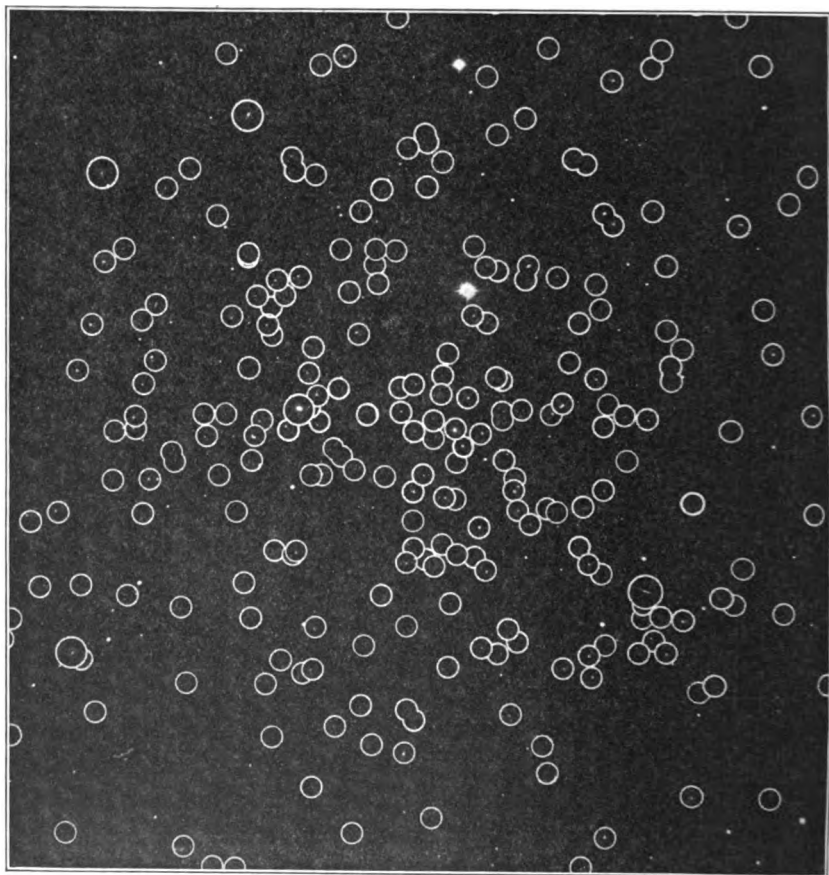


FIG. 2. Region of many small nebulae at $12^h 55^m + 28^\circ 30'$. 249 small nebulae in an area $38' \times 39'$.

ratio of the 60-inch would increase this disadvantage, even allowing for certain advantages which might partially counterbalance this due to the greater linear scale of the plates. The following com-

parisons of the aberrations of the image of an infinitely distant object in the focal plane of a single, perfect, parabolic mirror, as calculated from Schwarzschild's formulæ⁴ for the Crossley and the 60-inch reflectors, will illustrate this point.

THE CROSSLEY REFLECTOR; FOCAL RATIO = 1:5.8.

Dist. from Optical Axis.	Distortion by Field Curvature.	Distortion by Coma.
30'	2".8	10".1
41' (corner of plate)	5".2	13".7

THE 60-INCH REFLECTOR; FOCAL RATIO = 1:5.0.

30'	3".3	13".5
61' (corner of plate)	13".5	27".5

From my own experience in counting these minute objects on the Crossley plates it would appear to me that the actual *effective* area used by Fath must have been very much less than the 1.88 square degrees assumed by him in his calculations.⁵ It is my opinion also that the Lumière Sigma plates which he used are not the best for the end in view. These plates are of very great speed, and are invaluable for some purposes. I have long since ceased to use them for nebular work, however, believing that the slightly slower, but beautifully "clean" Seed 27 and Seed 23 plates really show the faintest details better. With the smaller grain and clear background existing in the Seed plates, very small and faint nebulae "stand out" much more plainly than on the more rapid Sigma plates.

D. It is not impossible that a considerable proportion of the thirty or so plates which Fath took within 45° of the north galactic pole happened to strike regions of comparatively few small nebulae. Had he chanced to include four such regions as the following:

⁴ Untersuchungen zur geometrischen Optik," *Abh. Kön. Ges. d. Wiss. zu Göttingen, Math.-Phys. Kl.*, N. F., 4, 1, 2, and 3, 1905.

⁵ Since the completion of the manuscript of this paper Dr. Fath has published a note on "The Probable Number of Nebulae" in *A. J.*, 728, March 12, 1918, in answer to a letter in which Dr. Perrine had called his attention to the large angular area and the increased parabolic distortions in the outer parts of the plates as a factor in the smaller estimate made by Dr. Fath. Dr. Fath finds, by taking the counts found from the areas 40' square in the center of the Mt. Wilson plates, that there is a marked increase in the number of nebulae found, amounting to about 60 per cent., and increasing his earlier estimate to 262,000.

^{a.}	^{b.}	No. of Small Nebulæ.
11 ^h 9 ^m + 55° 34'	107
11 ^h 22 ^m + 17° 46'	69
12 ^h 15 ^m + 6° 1'	81
12 ^h 55 ^m + 28° 30'	304
		<hr/> 561

his estimate would have been increased by at least 60 per cent. (he found 864 new nebulæ in all, and the larger plates he used would have added a number to those counted on the Crossley plates).

Perhaps all the reasons outlined above may be regarded as contributing to an explanation of the difference between Fath's estimate of 162,000, and the larger ones due to Perrine and the present investigation. Of these, the possibility noted under (*B*), that the small nebulæ may conceivably occur in greatest profusion contiguous to the visually discovered objects of the N. G. C., would appear to be the only reason for changing the larger estimates, and this evidence is only to be secured by taking many additional plates at random.

In conclusion, I see no reason, at present existing, for changing the estimate made in this paper, that at least 700,000 small spirals are within reach of large reflecting telescopes. Because of the fact that the faintest and smallest members of the class are, in general, discernible only in the more central regions of the plate, I am inclined to regard the figure given above as, if anything, an underestimate, and consider it very probable that the total number accessible may well exceed one million.

PROCEEDINGS

OF THE

American Philosophical Society

HELD AT PHILADELPHIA

FOR PROMOTING USEFUL KNOWLEDGE

Vol. LVII.

1918.

No. 6.

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PHILADELPHIA

THE AMERICAN PHILOSOPHICAL SOCIETY

104 SOUTH FIFTH STREET

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TO THE SECRETARIES OF THE

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PHILADELPHIA, U S A.

THE NAYADES (FRESHWATER MUSSELS) OF THE
UPPER TENNESSEE DRAINAGE. WITH NOTES
ON SYNONYMY AND DISTRIBUTION.

By A. E. ORTMANN, PH.D., Sc.D.

(Read April 19, 1918.)

The present enumeration of the mussels of the upper Tennessee is the result of the writer's work carried on in this region since 1912, under the auspices of the Carnegie Museum of Pittsburgh, Dr. W. J. Holland, director.

It is intended, herein, to give a complete synopsis of this fauna, using the modern system, and the accepted rules of nomenclature, together with a full synonymy of the various forms, as far as it has been firmly established. Much stress has been laid upon the facts of the geographical distribution, because it has become evident that not all of the species are uniformly distributed in this area.

The latter includes all of the upper Tennessee drainage from Chattanooga, Tenn., upward, comprising largely eastern Tennessee, a small section of northern Georgia, and parts of North Carolina (in the high mountains), and southwestern Virginia. It appears that the Walden Gorge of the Tennessee River, below Chattanooga, forms some kind of a barrier to Nayad distribution, at least for certain species; at any rate, it forms a natural division within the Tennessee system. Of course, not all parts of this drainage have been investigated by myself; but collections have been made in all of the more important streams; and, together with the records obtained from other sources, it is believed that this fauna is now rather completely known.

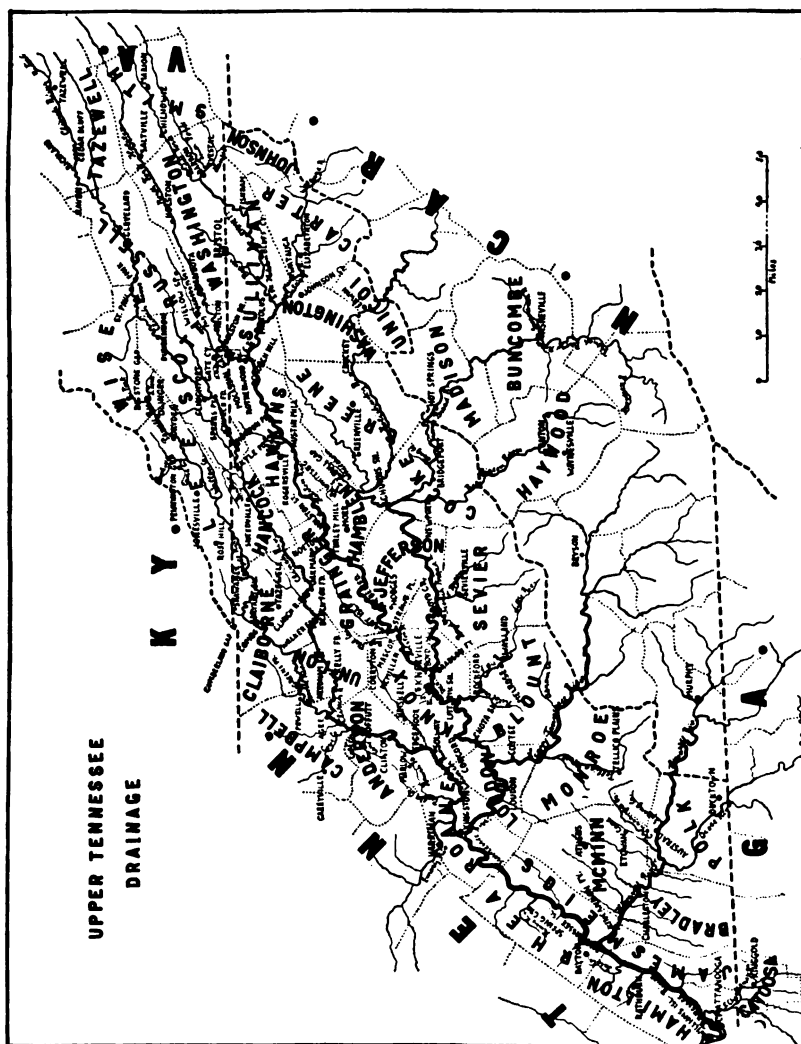
The region in question is known as one of the chief centers of Nayad development, and may be called the most prolific section of the world in this particular group. Many of the species described by the older authors (Conrad, Lea, and others) originally came from this region. But no synopsis of the whole fauna has been published, except the attempt made by Lewis (1871 and 1872).

In this connection it should be noted that Lewis's "Holston River" actually is the Tennessee River below Knoxville (chiefly in the region of Concord). Indeed, even at present, the natives in Concord call the river there "Holston"; but the maps of the U. S. Geological Survey give the name Tennessee to the river below the junction of the Holston (proper) and French Broad. In Knoxville the river is called Tennessee.

Aside from Lewis's paper, only a few are at hand which contribute to the fauna of this region. One of them has been published by Pilsbry and Rhoads (1896). This is, however, by no means a synopsis, containing hardly half of the forms which are found here. But on account of the good locality-records it is very valuable; in fact, it is, up to the present time, the most accurate publication in this respect. And further, two preliminary papers have been published, based upon my own collections; one by myself (Ortmann, 1913*b*), the other by Goodrich (1913). These, however, treat only of the headwaters-region of Powell, Clinch, and Holston in Virginia.

In addition to the material collected by myself, I have examined the upper Tennessee shells in the collection of Mr. B. Walker in Detroit, and I want to express to Mr. Walker my best thanks for the privilege of examining his shells, and the delightful days I spent in his home in April, 1916. Mr. Walker has a great number of shells from this region obtained from older collections, which in part are cotypes, topotypes, or other authentic material. But the greatest treasure in his collection are the *Nayades* collected by Professor Dr. C. C. Adams in 1899 to 1901, in the course of his work on *Io*, because Professor Adams always was very careful in recording his localities.

A large number of the "species" described by Lea (generally from very insufficient material), and of those listed by Lewis, are synonyms. Additional species have been subsequently described by various authors; but also these are mostly synonyms. There is a rule, observed in many cases, and indicated first by Wilson & Clark, '14, that one and the same shell assumes different shapes in the large rivers and in small streams and headwaters, a rule the existence of which will be shown elsewhere; and it is easily understood why the various local races have been regarded as good species, as long as



the intergrades were not known. But the discovery of the latter—and this was one of the problems to which I directed my attention—has necessitated the cancellation of a great number of these nominal species. Nevertheless, the fauna still remains remarkably rich, which surely in a large part is due to the comparatively old age of this river system, to the diversity of its character, and also to certain changes of the drainage which have taken place in the geological past.

In the following pages, the correct names of the various forms are given, conforming to the systematic arrangement published by the writer (Ortmann, 1910, 1912*b*), and conforming with the rules of priority. It should be remarked, that of practically all Tennessee-forms the anatomy has been investigated, but has not yet been published of all of them: the description of the rest will appear in due time. The two great papers of Simpson (1900 and 1914) are taken as a basis, and the quotations are from the last paper, so that it can be easily seen, where changes in nomenclature have been introduced. Also the names used by Lewis, those used by Pilsbry and Rhoads, by myself and Goodrich are given, in order to facilitate comparison with our list. The synonyms are all quoted unless they have been recognized and accepted as such by Simpson; but other references have been largely omitted, for the reason that they generally are found in Simpson's paper.

No full descriptions of the forms are given, but frequently the chief characters are briefly indicated.

The extralimital distribution has not been given in detail. Here and there it has been referred to, but only in especially interesting cases. In this respect, much work remains to be done, and in many North American Nayades the exact boundaries of the distribution have not yet been exactly located.

The material, upon which the present paper is founded, has been deposited in the Carnegie Museum of Pittsburgh, and comes chiefly from the collections made by myself; a very small part has come from other sources. The Carnegie Museum is in possession of the old collections of Hartman, Holland, and Juny, and a more recent collection has been bought from H. H. Smith. In addition, the museum is indebted to Messrs. Frierson and Walker for occasional

exchanges of rare forms. As has been mentioned above, also Walker's collection has been examined, and incidentally some of the material of the U. S. National Museum, in Washington, chiefly some of Lea's types, has been studied.

It is believed that the Carnegie Museum possesses now the best collection representing the Upper Tennessee fauna, and with regard to the illustration of the distribution of the various forms, it has no equal, not to speak of the fine collection of soft parts. In view of the gradual, slow but steady, deterioration of the fauna in consequence of stream-pollution, there is great danger that the fauna will largely become destroyed, and that it will be impossible, in the future, to duplicate this collection. At the present time, conditions are fair, in some parts splendid; but there are already polluted streams, in which the fauna is gone. Such are: the Powell River, for a certain distance below Big Stone Gap, Va. (wood extracting plant); the North Fork Holston for a distance below Saltville, Va. (salt and plaster of Paris industries); French Broad River at Asheville, N. Car. (pollution comes—as I have been informed—from Davidson River, farther up); Big Pigeon River, from Canton, N. Car., all the way down (woodpulp and paper mill); Tellico River below Tellico Plains, Tenn. (old wood pulp and extracting mill). The building of dams (for water power, etc., for instance in Nolichucky River near Greenville, Tenn.) also has a deteriorating effect upon mussel life, and all this surely will increase in the future.

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Family: *MARGARITANIDÆ* Ortmann (1911a, p. 129).

Genus: *CUMBERLANDIA* Ortmann (1912a, p. 13).

1. *CUMBERLANDIA MONODONTA* (Say), 1829.

Unio monodonta Say, '29.—*Unio monodontus* Lewis, '71.—*Margaritana monodonta* Ortmann, '12b, p. 233 (anatomy).—*Margaritana monodonta* Simpson, '14, p. 521.

Widely distributed in the larger and medium rivers: Tennessee, Clinch, and Holston. According to Walker ('11), it goes up, in the Clinch, to Union Co., Tenn., but I found it also at Clinch River Station, Claiborne Co. In the Holston, I have traced it up to Austin Mill, Hawkins Co., Tenn. Walker gives it also from Little River, but this can be only in the lower part of it.

This is generally regarded as a rare species; but in the lower Clinch, in Anderson Co., and in the lower Holston, in Knox Co., Tenn., it is locally abundant.

Type locality: Falls of the Ohio.

Family: *UNIONIDÆ* Ortmann (1911a, p. 129).

Subfamily: *UNIONINÆ* Ortmann (1910, p. 116).

Genus: *FUSCONAIA* Simpson (1900).

Ortmann (1912b, p. 240).

2. *FUSCONAIA PILARIS* (Lea), 1840.

Unio pilaris Lea, '40.—*Unio globatus* Lea, '71.—*Unio ebenus* and *pilaris* Lewis, '71 and '72.—*Unio pilaris* Pilsbry & Rhoads, '96.—*Quadrula andrewsi* Marsh, '02.—*Quadrula beauchampi* Marsh, '02.—*Quadrula pilaris, andrewsi, beauchampi, globata* Simpson, '14, pp. 893-899.

This is the upper Tennessee representative of *F. subrotunda* Lea of the Ohio drainage, and it may be merely a dwarfed, globular form

of the latter. I have seen the normal *subrotunda* from the Tennessee in northern Alabama, but I cannot tell whether the two pass into each other.

The typical form of *F. pilaris* passes into the following local races in an upstream direction, and it is hard to draw a line between them. In order to preserve the oldest names given, I have arbitrarily concluded to call by this name those more swollen forms where the transverse diameter of the shell is 55 per cent. of the length and over.

This typical *F. pilaris* is restricted to the large rivers: Tennessee, lower part of Little Tennessee, lower French Broad, lower Holston and lower Clinch. In the two latter rivers it is rare, and intergrades with the next form, going up, in the Holston, to Grainger Co., and in the Clinch, to Anderson Co., Tenn.

Type locality: French Broad River, Tenn., and Holston River, Tenn. (topotypes examined).

3. *FUSCONAIA PILARIS LESUEURIANA* (Lea), 1840.

Unio lesueurianus Lea, '40.—*Quadrula flexuosa* Simpson, '00.—*Quadrula flexuosa* Simpson, '14, p. 887.

According to Simpson, '14, p. 894, *lesueuriana* is synonym to *pilaris*.

Like *pilaris*, but less swollen; the diameter of the shell is from 45 per cent. to 54 per cent. of the length.

Of *Q. flexuosa*, I have seen, in the Walker collection, two specimens from Holston River, Knoxville (Mrs. Andrews), and one specimen from Holston River, Hamblen Co. (opposite Grainger Co.) (Marsh). They had been compared with the type of *flexuosa*, and thus labeled by Marsh. Two of these, with the diameter of 53 and 54 per cent., are *lesueuriana*, while one (Knoxville), with diameter of 56 per cent., is *pilaris*. Simpson's measurements of *flexuosa* give the diameter of 51 per cent., and thus it should be made a synonym of *lesueuriana*.

This is the form of the medium rivers; it turns up in single individuals in the region of Knoxville, and becomes the prevailing form in the lower Clinch and in the whole Holston proper. In the Clinch, it has been traced up, in single individuals, to Scott Co., Va., and it

also goes into the lower Powell, up to Claiborne Co., Tenn. From the Holston, it goes in the lower parts of the North and South Fork: but at and near its upper limit, it always intergrades with the next form (*bursa-pastoris*).

Type locality: Caney Fork River, Tenn. (and Holston River, Tenn.). (Thus it seems to exist also in the Cumberland drainage, but this requires further investigation. Wilson and Clark, '14, do not mention it.)

4. *FUSCONAIA PILARIS BURSA-PASTORIS* (Wright), 1896.

Unio bursa-pastoris Wright, '96.—*Unio kirtlandianus* Pilsbry & Rhoads, '96.—*Fusconaia bursa-pastoris* Ortmann, '13a, p. 90 (anatomy), and '13b, p. 311.—*Fusconaia bursa-pastoris* Goodrich, '13, p. 93.—*Quadrula bursa-pastoris* Simpson, '14, p. 890.

This is the compressed headwaters-form of *F. pilaris*, connected with it through the intermediate form *lesueuriana*. It has the same relation to *F. pilaris*, as has *F. kirtlandiana* (Lea) of the upper Ohio drainage to *F. subrotunda*; it is practically the same thing, except that it does not reach the size of it, and does not develop the "wing" seen on the posterior upper margin of *kirtlandiana*. It is perfectly clear that the form mentioned by Pilsbry & Rhoads from Watauga River, Johnson City, Tenn., is this, and, indeed, I have found it very close to this locality.

The diameter of this form is less than 45 per cent. of the length, and it appears as if the lack in this direction is compensated by a greater circumference of the shell, *bursa-pastoris* often reaching a size (length and height) not seen in either *pilaris* or *lesueuriana*.

The metropolis of this form is in Clinch River; a few specimens have been found in the lower Clinch, in Knox and Anderson Cos. (associated with *lesueuriana* and even *pilaris*); farther up, from Claiborne Co., Tenn., into Virginia, it becomes more and more abundant, and north of the state line, where *lesueuriana* disappears (only found at Clinchport), it is developed as a pure race, going up into the headwaters as far as Cedar Bluff, Tazewell Co., Va. In Powell River, similar conditions prevail; in the lower Powell it is found associated and intergrading with *lesueuriana*, but north of the

state line, in Virginia, it is exclusively present, going up to Big Stone Gap, entering even a small tributary (Cane Creek, Lee Co., Va.).

In the Holston, this form is not so well developed, and not so abundant, but is present nevertheless, and also has the same relation to *lesueuriana*, first being associated with it, but then being exclusively present. The latter is the case in North Fork Holston, in Washington Co., Va. In South Fork Holston, it goes up to Bluff City, Sullivan Co., Tenn., but accompanied by *lesueuriana*; but it enters here Wautauga River, where it is found alone. In the Holston proper, in a downstream direction, it is quite rare, but it has been found as far down as Grainger Co., so that in this region (as is the case in lower Clinch) occasionally all three forms of the species may be obtained together.

Type locality: Powell River, Va. (topotypes examined).

Note: The color of the soft parts and eggs in the *pilaris* group varies greatly. The soft parts may be of the orange type, and the eggs (and placentæ) may be red: this is chiefly the case in Powell and upper Clinch rivers. Elsewhere, in Holston, French Broad, and Tennessee, pale soft parts, with whitish eggs prevail.

5. *FUSCONAIA CUNEOLUS* (Lea), 1840.

Unio cuneolus Lea, '40.—*Unio cuneatus* Reeve, Conch. Icon. 16.

Unio, '64, pl. 16, f. 73.—*Unio cuneolus* Lewis, '71.—*Unio cuneolus* Pilsbry & Rhoads, '96.—*Pleurobema cuneolus* Simpson, '14, p. 743.

This is not a *Pleurobema*, but a *Fusconaia*, taking the place of the group of *F. flava* (Raf.) (= *rubiginosa* Lea) in the upper Tennessee region. It is a very good species.

The original and typical *cuneolus* represents a compressed head-waters-form, which, farther down, changes into a more swollen form. I have, arbitrarily, decided to call specimens with the diameter less than 50 per cent. of the length by this name.

This form is found in Powell, Clinch, and Holston rivers, in the upper parts. In the Powell, from Union Co., Tenn., up to Olinger, Lee Co., Va. (also in Puckell Creek, Lee Co.); in the Clinch from Anderson Co., Tenn., up to Clinchport, Scott Co., Va.; in the Holston

from Grainger Co., Tenn., up the North Fork at Mendota, Washington Co., Va., and Big Moccasin Creek, Scott Co., Va. It has not been found in South Fork Holston, Watauga, or any of the eastern tributaries of the Tennessee, although the var. *appressa* goes to the lower Nolichucky and into the Little River drainage.

In addition, it is in some of the tributaries of the lower Clinch: in Poplar Creek, Roane Co. (intergrading here with *cuneolus appressa*) and in Emory River, at Harriman, Roane Co., Tenn.

Type locality: Holston River, Tenn. (topotypes examined).

6. *FUSCONAIA CUNEOLUS APPRESSA* (Lea), 1871.

Unio appressus Lea, '71.—*Unio tuscumbiensis* Lea, '71.—*Unio flavidus* Lea, '71.—*Pleurobema tuscumbiensis* Simpson, '14, p. 748.

There has been great confusion about this form, for the reason that the type-set in the U. S. Mus. (examined by myself) contains three specimens, of which only one, the figured type, is this, while the other two belong to *Lexingtonia dolabelloides conradi* (Van.). But several authors seem to have taken the latter as the types, and thus, for instance, *Pleurobema appressum* Simpson ('14, p. 747) is not this, but *Lexingtonia dolabelloides conradi*.

The figured type of Lea is a more swollen form of *F. cuneolus*, and resembles the latter in every respect except obesity. I have drawn the line between the two at the diameter of 50 per cent. of the length, and specimens with this diameter, and over, I call *F. cuneolus appressa*.

This variety belongs to the larger rivers. I have not seen it from the Powell, and in the Clinch it turns up for the first time below the mouth of the Powell, at Offutt, Anderson Co., Tenn., but it goes into a smaller tributary of the lower Clinch, Poplar Creek, Roane Co., associated here with typical *cuneolus*. In Emory River, only *cuneolus* has been found. In the Holston, *appressa* turns up first at Austin Mill, Hawkins Co., Tenn., associated and intergrading with typical *cuneolus*. I also found *F. cuneolus appressa* in the Nolichucky, at its mouth, and then it seems to be the prevailing form in the Tennessee at and below Knoxville.

Remarkably enough, I have found a single specimen of this form in a very small creek tributary to Little River—Pistol Creek, Rockford, Blount Co., Tenn.—it has the diameter of 50 per cent., and thus stands just on the line dividing the two varieties. This specimen is rather stunted in growth, and may be only an individual abnormality.

Type locality: Tuscumbia, Ala. (Tennessee River and Holston River, Tenn.) (type examined).

Note: This type of shell is also present in the Tennessee drainage in North Alabama, where again the *appressa*-form inhabits the larger rivers, while in the smaller streams typical *cuneolus* is found.

7. FUSCONAIA COR (Conrad), 1834.

Unio cor Conrad, '34.—*Unio edgarianus* Lea, '40.—*Unio obuncus* Lea, '71.—*Unio edgarianus* Lewis, '71.—*Unio andersonensis* Lea, '72.—*Unio edgarianus* Pilsbry & Rhoads, '96.—*Pleurobema edgarianum* Simpson, '14, p. 741.

According to Frierson (Naut., 29, '16, p. 102 ff.) the type of *U. cor* Conrad is the same as shells which have been called *edgarianus*, *tuscumbiensis*, *andersonensis*. Frierson has sent for inspection a specimen, which had been compared with the type of *cor*, and this proved to be *edgarianus*. This is also supported by Conrad's description, which says that *cor* has rays, some of them broad.

This species is closely allied in shell and anatomy to *F. cuneolus*, but is distinguished by very smooth and shining epidermis, and by beautiful color: upon a brownish or yellowish background are bold, dark green to blackish rays, while *cuneolus* has greenish or yellowish-olive epidermis, with finer, greenish rays.

The original *cor* is a much swollen form, and belongs to the larger rivers; but in the smaller streams, it again passes into a more compressed form (*F. cor analoga*). I have drawn the line between the two at the diameter of 50 per cent. of the length, so that specimens with this or a greater diameter fall under *cor*.

I have found this form only in Clinch River, at Edgemoor, Anderson Co., Tenn., and, according to Pilsbry & Rhoads, it is in the Clinch in Roane Co. In the Walker collection, there are specimens belonging here from Needham Ford, Union Co., Tenn. (associated

with var. *analoga*). In the same collection are typical *cor* also from Poplar Creek, Roane Co., a rather small stream, where we should expect the headwaters-form. (It happens, sometimes, that a small tributary of a large river has, at or near its mouth, the large-river form.) Lewis reports this form from the Tennessee below Knoxville.

Type locality: Elk River, Ala. (and Flint River, Ala.) (topotypes examined, loaned by Frierson).

Note: Conrad's Flint River is not the one in Madison Co., but the one in Morgan Co., Ala.

8. FUSCONAIA COR ANALOGA nov. var.

Unio edgarianus Reeve, Conch. Icon. 16. Unio. 1864, pl. 15, f. 65.—

Fusconaia appressa or *edgariana* Goodrich, '13, p. 93.

This flat form of *cor* (or *edgarianus*) has never been separated from the swollen typical form, probably because there never was any doubt about its affinity, on account of the peculiar color character of the shell. However, it differs from typical *cor* as strongly as does *F. cuneolus* from *F. cuneolus appressa*, and thus deserves a varietal name. The shell figured by Reeve as *U. edgarianus* surely is this, since the compressed shape is mentioned. Specimens with the diameter less than 50 per cent. of the length fall under this variety.

This is the form of the headwaters and small streams. It is in the Powell, and goes up to Lee Co., Va. It is in the Clinch, from Needhams Ford, Union Co., Tenn. (Walker coll.) up to Cleveland, Russell Co., Va., and becomes quite abundant in the Virginian part of this river. In addition, it is in the North Fork Holston from Hawkins Co., Tenn., up to Holston, Washington Co., Va.

It has never been found in any other part of the Holston drainage, or any other river or creek in East Tennessee, and its restriction to North Fork Holston, Clinch, and Powell, and its continuation downward, as typical *cor*, in the Tennessee proper alone, is quite remarkable.

Type locality: Clinch River, Speers Ferry, Scott Co., Va. (types in Carn. Mus. Cat. no. 61.6326).

Note: The group of *F. cor* is also represented in the Tennessee

drainage of North Alabama, and, also here, *cor* is in the Tennessee proper and the lower parts of the larger tributaries (Elk, both Flint, and Paint Rock Rivers), while in the upper parts, at least of Paint Rock River, it passes into the *analoga*-form.

GROUP OF *FUSCONAIA BARNESIANA* (Lea).

Forms of this group have been listed by Lewis ('71) as *U. barnesianus*, *pudicus*, and *tumescens*. In Simpson's papers ('00 and '14), they stand under *Pleurobema*, and their proper position and mutual relation have not at all been understood.

All these shells belong to *Fusconaia*, but form a separate group within this genus, distinguished from the other species by very shallow beak cavities, and the peculiar color of the eggs and placenta, which is darker or lighter purplish-black, or some similar shade (see Ortmann, '17).

Also here we have the phenomenon that flat and compressed forms are found in the headwaters, swollen forms in the larger rivers, with the intergrades between them in the rivers of medium size. The transition is complete and very gradual, so that it is extremely difficult to draw separating lines. The division into three local (or rather ecological) races, introduced here, is entirely arbitrary, but justified to a degree by the old division into "species," and the fact that it is just such an intergrade which has first received a name (*barnesianus*). The difficulty of classifying these forms becomes greater yet, because these shells vary not only in obesity, but also in general outline, development of beaks, and color markings.

I shall distinguish three forms: *barnesiana bigbyensis*, with the diameter less than 40 per cent. of the length; *barnesiana*, with the diameter from 40 to 49 per cent.; and *barnesiana tumescens*, with the diameter of 50 per cent. and over.

9. *FUSCONAIA BARNESIANA* (Lea), 1838.

Unio barnesianus Lea, '38.—*Unio meredithi* Lea, '58.—*Unio pudicus* Lea, '60.—*Unio lyoni* Lea, '65.—*Unio barnesianus* and *pudicus* Lewis, '71.—*Unio tellicoensis* Lea, '72.—*Unio lenticularis* Lea, '72.—*Pleurobema barnesianum*, *pudicum*, *lenticulare*, *meredithi*

Simpson, '14, pp. 754, 755, 790, 791.—*Fusconaia barnesiana* Ortmann, '17, p. 59.

Simpson, '14, p. 754, makes *tellicoense* a synonym of *barnesianum*, and (p. 755) *lyoni* a synonym of *pudicum*.

U. pudicus is practically the same as *barnesianus*, but with distinct rays; *meredithi* is a *pudicus* with only few rays; *U. lyoni* is large and has rays; it also has somewhat elevated beaks, inclining thus toward the var. *tumescens*; *tellicoensis* and *lenticularis* are moderately large, with indistinct rays, practically identical with *barnesianus*.

This form, which we must regard as the typical species, unfortunately represents the intermediate condition between the flat and swollen extremes. It is represented by shells from the Powell, Clinch, and Holston, going up here well toward the headwaters: in Powell to Big Stone Gap, Wise Co., Va.; in the Clinch to Richland, Tazewell Co., Va.; in the Holston to the North Fork at Holston, Washington Co., Va., and to the South Fork at Bluff City, Sullivan Co., Tenn. In the downstream direction, it can be traced to the Tennessee River below Knoxville. However, it is most abundant in lower Powell, in the middle Clinch, and in the Holston near the Forks. In addition, it turns up in many tributaries: Cove Creek, Campbell Co., Tenn.; Coal Creek, Anderson Co., Tenn.; Big Flat Creek, Knox Co.; in Little Pigeon River, Boyd Creek, Pistol Creek, Tellico River, Cane Creek (McMinn Co.), Hiwassee River, etc.

It is a common form, of rather universal distribution under the proper conditions. Toward the headwaters, it passes generally into the var. *bigbyensis*, but there are some small creeks where this is not the case (at any rate, where the *bigbensis*-form has not been found). In the larger rivers it gradually passes into the form *tumescens*, and is often found associated with it.

Type locality: Cumberland River, Tenn. (not found by Wilson and Clark, '14, although they mention "*Fleurobema crudum*" = *barnesiana tumescens*; the latter, however, surely has been misidentified).

10. *FUSCONAIA BARNESIANA BIGBYENSIS* (Lea), 1841.

Unio bigbyensis Lea, '41.—*Unio estabrookianus* Lea, '45.—*Unio fassinans* Lea, '68.—*Unio fascinans* Pilsbry & Rhoads, '96.—*Pleurobema fassinans rhomboidea* Simpson, '00.—*Fusconaia estabrookiana* Goodrich, '13, p. 93.—*Pleurobema bigbyense*, *P. fassinans* and var. *rhomboideum*, *P. estabrookianum* Simpson, '14, pp. 756, 797, 798, 803.—*Fusconaia barnesiana bigbyensis* Ortmann, '17, p. 59.

This is the form of the headwaters and small tributaries of the Tennessee system, with a diameter of less than 40 per cent. of the length of the shell. *U. bigbyensis* and *P. fassinans rhomboideum* represent normal specimens, the former with distinct, the latter with indistinct or missing rays. *U. estabrookianus* is founded upon very large, somewhat distorted specimens; and the only type (examined in Washington) of *U. fassinans* is an exceptionally elongated, rather large specimen without rays.

Also in this form we have the phenomenon that the compressed headwaters shell, so to speak, gains in circumference what it has lost in diameter. The var. *bigbyensis* grows much larger than the forms farther downstream. It is very variable in size, shape, color, and sometimes it is hard to distinguish it from *Pleurobema oviforme argenteum*. Generally, darker (brownish) color of epidermis, with fine rays (when present), forming no blotches, and a more central position of the beaks distinguish *F. barnesiana bigbyensis*. Of course, the anatomy is entirely different.

This race is very generally distributed over the whole upper Tennessee drainage, but disappears in the larger rivers. It often is in very small streams of the headwaters (North Fork Powell, and other small streams in the Powell drainage; in the Clinch at Tazewell, Va.; Big Moccasin Creek, all three forks of the Holston, and also Laurel Creek, Watauga River, and Little Pigeon River; Second Creek at Knoxville; Sale Creek in Rhea Co.; Little River; Abram Creek in Blount Co.; Tellico River; Spring Creek, Polk Co., and Cane Creek, McMinn Co.).

As has been stated, even at the uppermost localities, in very small creeks, *F. barnesiana* in its typical form may be present, and may be

associated with *bigbyensis*. Farther down, *barnesiana* soon begins to prevail. The form *bigbyensis* has been traced down in the Powell to Combs, Claiborne Co., Tenn.; in the Clinch to Clinchport, Scott Co., Va.; but a single specimen has been found at Solway, Knox Co., Tenn., apparently an exceptional case; in the Holston it has not been found below the point where the North and South Fork unite.

Type locality: Big Bigby Creek, Maury Co., Tenn. (trib. to Duck River and lower Tennessee).

11. *FUSCONAIA BARNESIANA TUMESCENS* (Lea), 1845.

Unio tumescens Lea, '45.—*Unio crudus* Lea, '71.—*Unio radiosus* Lea, '71.—*Unio tumescens* Lewis, '72.—*Unio tumescens* Pilsbry & Rhoads, '96.—*Pleurobema tumescens* and *P. crudum* Simpson, '14, p. 751, 753.—*Fusconaia barnesiana tumescens* Ortmann, '17, p. 59.

(Simpson makes *radiosus* a synonym of *tumescens*.)

This is the swollen form of the large rivers, with a diameter of 50 per cent. of the length, and over. It also generally has higher beaks, making the outline of the shell more nearly triangular; but higher beaks are also sometimes observed in the typical *F. barnesiana* (*lyoni*-type). *U. tumescens* represents the extreme in obesity, and *radiosus* (type examined!) is very close to it. *U. crudus* is the much eroded form of the French Broad River (topotypes at hand). The two former have more or less developed rays, the latter is rayless.

F. barnesiana tumescens has its metropolis in the Tennessee River at and below Knoxville. But it is also found some distance in the rivers above this point. From the Clinch it is known from the lower part; the uppermost locality is at Edgemoor, Anderson Co. It also has been reported (by Pilsbry and Rhoads) from Emory River at Harriman, Roane Co. In the Holston proper I have observed it as far up as Noeton, Grainger Co. It is also in the lower French Broad, at Boyd Creek, Sevier Co., in the Little Tennessee in Monroe Co., and in Hiwassee River, at Austral, Polk Co. (intergrading, at these places, with typical *F. barnesiana*).

Remarkably enough, a small tributary of Little River, Pistol Creek, Rockford, Blount Co., Tenn., contains shells, most of which,

according to actual measurements, should be classed with *tumescens*. But these shells are more or less distorted and stunted, and apparently abnormal; those of more normal growth correspond in their measurements to *barnesiana*.

Type locality: "Alexandria, La." This is surely incorrect. Specimens from the Tennessee River in northern Alabama have been recognized as this form by Call, Pilsbry and Rhoads, and Walker; and Lewis ('72), and Pilsbry and Rhoads quote it from East Tennessee, and I think this identification is quite correct.

Note: In northern Alabama, in the Tennessee drainage, and generally below the Walden Gorge, this type of shell is also abundant, and again here we have the *tumescens*-form in the Tennessee proper and the lower parts of some of the tributaries (Sequatchie River, Shoals Creek). Farther up in the tributaries, typical *barnesiana* prevails, and the *bigbyensis*-form is in the smallest streams. Forms belonging to the latter, corresponding closely to *fassinans rhomboideum*, and the large *estabrookianus*-type of the upper Powell, Clinch and Holston, have come to hand from the headwaters of Paint Rock River and Elk River (Estill Springs). In Shoals Creek, Lauderdale Co., Ala., a very peculiar mixture is found, containing all three types side by side, intergrading completely, but with the typical *barnesiana* prevailing.

Genus: AMBLEMA Rafinesque, 1820.

Crenodonta (Schlueter, '36), Ortmann, 1912b, p. 245.—*Amblesma* Frierson, 1914a, p. 7.

12. AMBLEMA PLICATA COSTATA (Rafinesque), 1820.

Amblesma costata Rafinesque, '20.—*Unio undulatus* Lewis, '71.—*Unio undulatus* Pilsbry & Rhoads, '96.—*Crenodonta undulata* Ortmann, '12b, p. 246 (anatomy).—*Crenodonta undulata* Goodrich, '13, p. 93.—*Quadrula undulata* Simpson, '14, p. 819.—*Amblesma costata* Frierson, '14a, p. 7.—*Quadrula costata* Vanatta, '15, p. 556.—*Amblesma (plicata) costata*, Utterback, '16, p. 39.

As to nomenclature, see Frierson and Vanatta (*l. c.*). The identity of Rafinesque's species has been recognized already by Conrad in

1834 and 1836, and the name of *costata* has been used by Kuester and Reeve. Moreover, the true *U. undulatus* Barnes, '23, is actually *U. heros* Say, '29. *U. plicatus* Say, 1817, is the Lake Erie form (= *hippopæus* Lea, '45), and *costata* Raf. of the Ohio drainage, apparently is the ancestral form to this. But according to the laws of priority, *plicatus*, although being a local race, has to stand as the main species.

Generally distributed in the upper Tennessee drainage, in Powell, Clinch, lower Emory, Holston, French Broad, Nolichucky rivers, lower Little River, and Tennessee proper. Goes up to Shawanee, Claiborne Co., Tenn., in the Powell; to Cleveland, Russell Co., Va., in the Clinch; to Hilton, Scott Co., Va., in North Fork Holston; and Pactolus, Sullivan Co., Tenn., in South Fork Holston; to the mouth of the Nolichucky at Chunn's Shoals, Hamblen Co., Tenn. It also occasionally enters some rather small streams, for instance: Poplar Creek, Roane Co., and Boyd Creek, at Boyd Creek, Sevier Co., Tenn.

Type locality: Ohio River (Raf.) (according to Vanatta, the type is from small creeks in Kentucky).

Genus: *QUADRULA* Rafinesque, 1820.

Ortmann, 1912b, p. 250.

13. *QUADRULA PUSTULOSA* (Lea), 1831.

Obliquaria bullata Rafinesque, '20.—*Unio pustulosus* Lea, '31.—*Unio pernodosus* and *U. pustulosus* Lewis, '71.—*Unio pustulosus* and *sphaericus* Pilsbry & Rhoads, '96.—*Quadrula pustulosa* Ortmann, '12b, p. 251 (anatomy).—*Quadrula pustulosa* Simpson, '14, p. 848.

According to Vanatta ('15, pp. 556, 557), *Obliquaria retusa* Raf., '20, "probably" is *U. pustulosus* Lea, '31, and *O. bullata* Raf., '20, is *U. pernodosus* Lea, '45: but the latter is not different from *pustulosus*. The identity of *O. bullata* and *U. pustulosus* has been asserted by Conrad in 1834, and is evident from Rafinesque's description. Also Kuester and Reeve have used the name of *bullatus*. However, as Vanatta points out, the specific name *bullata* is preoccupied by

Obliquaria flexuosa bullata Raf., '20 (Internat. Rules of Zoöl. Nomencl., Art. 11), and since the identity of *O. retusa* is not quite certain, the name given by Lea becomes available.

I cannot see anything but an individual variation in what Lea has called *U. pernodosus*. This is given from "North Carolina," according to Lea probably from the tributaries of the Tennessee (in the mountains). But its occurrence in these parts has never been confirmed. *U. sphaericus* (?), reported by Pilsbry & Rhoads from near Chattanooga, surely is this.

This species prefers the larger rivers, and is not rare in them, chiefly so in the Tennessee at and below Knoxville. I traced it up the Clinch to Offutt, Anderson Co., Tenn., but a single specimen is in the Walker collection also from the Powell, at Bryant Shoals, Claiborne Co., Tenn. In the Holston, it goes up to McBee Ford, near Hodges, Jefferson Co., and in the French Broad, it reaches the lower part of the Nolichucky at Chunn's Shoals, Hamblen Co., Tenn.

Type locality: Ohio.

14. QUADRULA VERRUCOSA (Rafinesque), 1820.

Obliquaria verrucosa Rafinesque, '20.—*Unio conjugans* Wright, Naut., 13, '99, p. 89.—*Quadrula tuberculata* Ortmann, '12b, p. 254 (anatomy).—*Tritogonia tuberculata* and *T. conjugans* Simpson, '14, pp. 318, 322.—*Tritogonia verrucosa* Vanatta, '15, p. 554.—*Quadrula verrucosa* Utterback, '16, p. 62.

This form has been previously reported, as *U. conjugans*, only from Hiwassee River, and the type (examined in Washington) is indeed a remarkable shell, an apparently stunted, shortened male of this species (individual abnormality). That this species is actually present in the lower part of the Hiwassee, in Meigs Co., Tenn., is shown by three fine specimens in the Walker collection (Adams). It is very remarkable that I did not find a trace of this striking species in any other part of the upper Tennessee drainage.

Type locality: Ohio River.

Note: Below the Walden Gorge, in Sequatchie River, Tenn., and the Tennessee drainage in northern Alabama, this species is more abundant, both in the Tennessee River and its tributaries (Paint

Rock River, Flint River in Madison Co., Elk River, Shoals Creek, Bear Creek).

15. *QUADRULA METANERVA* (Rafinesque), 1820.

Obliquaria metanerva Rafinesque, '20.—*Unio metanerva* Lewis, '71.
—*Quadrula metanerva* Ortmann, '12b, p. 255 (anatomy).—*Quadrula metanerva* Simpson, '14, p. 834.

In the Tennessee at and below Knoxville. Above Knoxville, I found only a single specimen in the Holston, at Mascot, Knox Co. Rare.

Type locality: Kentucky River (according to Vanatta, '15, the types are from Ohio River).

16. *QUADRULA INTERMEDIA* (Conrad), 1836.

Unio intermedius Conrad, '36.—*Unio tuberosus* Lea, '40.—*Unio sparsus* Lea, '41.—*Unio intermedius, sparsus, tuberosus* Lewis, '71.—*Quadrula sparsa* Ortmann, '12b (anatomy).—*Quadrula intermedia* Goodrich, '13, p. 93.—*Quadrula tuberosa, tuberosa sparsa, intermedia* Simpson, '14, pp. 836, 837.

According to Simpson, *Q. tuberosa* is more swollen than *Q. intermedia*, and I have seen rather swollen specimens in the Walker collection from the Cumberland River and the Tennessee in North Alabama. However, the original figure of *U. tuberosus* Lea is not much swollen. My specimens from the upper Tennessee drainage are all more or less compressed. We might have here again a case where in larger rivers a more swollen form turns up. But even if this should be correct, we should only regard these forms as races of the same species.

Reported from Nolichucky, Holston, Clinch, and Tennessee rivers, and said to be abundant. According to the material collected and seen by myself, it is decidedly a rare species. I know it from the Holston at Church Hill, Hawkins Co., Tenn.; from the South Fork Holston at Pactolus and Bluff City, Sullivan Co., Tenn.; from North Fork Holston at Mendota, Washington Co., Va.; and from the Clinch River at Clinchport, Scott Co., Va. (Walker coll.), and Cleveland, Russell Co., Va.

It is remarkable that I did not find it in the lower parts of these rivers, although it has been reported from the Knoxville region, and from the Tennessee in northern Alabama.

Type locality: Nolichucky River, Tenn.

17. *QUADRULA CYLINDRICA* (Say), 1817.

Unio cylindricus Say, '17.—*Unio cylindricus* Lewis, '71.—*Unio cylindricus* Pilsbry & Rhoads, '96.—*Quadrula cylindrica* Ortmann, 12*b*, p. 256 (anatomy).—*Quadrula cylindrica* Simpson, '14, p. 832.

Reported from the Tennessee below Knoxville and from the Holston River. It is rather frequent in the larger rivers, and goes, in the Holston, up to Hawkins Co., Tenn. In the region of the forks it begins to incline toward the next form; however, in Big Mocassin Creek, Mocassin Gap, Scott Co., Va., a tributary of the North Fork, I found a rather normal *cylindrica*. In the Clinch, it goes to Clinchport, Scott Co., Va. It is also in the Powell, up to Claiborne Co., Tenn.

Type locality: Wabash River.

18. *QUADRULA CYLINDRICA STRIGILLATA* (Wright), 1898.

Unio cylindricus strigillatus Wright, Nautilus, 12, '98, p. 6.—*Quadrula cylindrica strigillata* Ortmann, '13*b*, p. 311.—*Quadrula cylindrica strigillata* Goodrich, '13, p. 93.

Simpson ('14, p. 834) does not admit this as a separate form; but it is a very good and well-marked local race, belonging to the headwaters, being compressed, devoid of large tubercles, but thickly covered with small ones.

Its metropolis is in the upper Clinch River. Intergrades between this and the main form are found in Scott Co., Va., and thence farther up, it becomes a pure race, and goes up to Cedar Bluff in Tazewell Co., Va. The same conditions prevail in Powell River, where it intergrades with the normal type in Claiborne Co., Tenn., and then goes up to Pennington Gap in Lee Co. It also exists in North Fork Holston, from Hawkins Co., Tenn., to Mendoto, Washington Co., Va., and in the South Fork Holston at Pactolus, Sullivan Co., Tenn.

But the specimens from the Holston drainage are not so well and typically developed as those from the upper Clinch.

Type locality: "Clinch River, Lee Co., Va." A case of inexcusable carelessness, for the Clinch never touches that county.

Genus: ROTUNDARIA Rafinesque (1820).

Ortmann, 1912*b*, p. 257.

19. ROTUNDARIA TUBERCULATA (Rafinesque), 1820.

Obliquaria tuberculata Rafinesque, '20.—*Unio verrucosus* Lewis, '71.—*Unio verrucosus* Pilsbry & Rhoads, '96.—*Rotundaria tuberculata* Ortmann, '12*b*, p. 258 (anatomy).—*Quadrula (Rotundaria) tuberculata* Simpson, '14, p. 903.

Abundant in the larger rivers, going rather far up toward the headwaters. The extreme points are: Clinch River, Clinchport, Scott Co., Va.; North Fork Holston River, Mendota, Washington Co., Va.; South Fork Holston River, Pactolus, Sullivan Co., Tenn.; Nolichucky River, Chunn's Shoals, Hamblen Co., Tenn. I have it also from Boyd Creek at Boyd Creek, Sevier Co., Tenn., a very small tributary of French Broad.

In the other eastern tributaries of the Tennessee (Little River, Little Tennessee, and Hiwassee) it has not been found, and also no records are at hand from Powell River.

Type locality: Ohio River.

Genus: PLETHOBASUS Simpson (1900).

Ortmann, 1912*b*, p. 259.

20. PLETHOBASUS COOPERIANUS (Lea), 1834.

Unio cooperianus Lea, '34.—*Unio cooperianus* Lewis, '71.—*Unio cooperianus* Pilsbry & Rhoads, '96.—*Plethobasus cooperianus* Ortmann, '12*b*, p. 261 (anatomy).—*Quadrula cooperiana* Simpson, '14, p. 852.

In the Tennessee River at and below Knoxville, down to Chattanooga (Pilsbry & Rhoads). Also in the lower Clinch River; I have

it from Edgemoor, Anderson Co., Tenn., and Pilsbry and Roads give it from Patton's Ferry, Roane Co., Tenn. I also have found it in French Broad River, at Boyd Creek, Sevier Co., Tenn. Records from "Holston River" probably refer to the Tennessee, at any rate, it must be a rare shell above Knoxville.

Type locality: Ohio River.

21. PLETHOBASUS CYPHYUS (Rafinesque), 1820.

Obliquaria cyphya Rafinesque, '20.—*Unio æsopus* Lewis, '71.—*Plethobasus æsopus* Ortmann, '12b, p. 260 (anatomy).—*Pleurobema æsopus* Simpson, '14, p. 806.—*Pleurobema cyphia* Vanatta, '15, p. 556

In the larger rivers, Tennessee, Clinch, Powell, Holston, and French Broad, going up, in the Powell, to Bryant Shoals, Claiborne Co., Tenn.; in the Clinch to Clinchport, Scott Co., Va.; in the Holston to the mouth of the North Fork at Rotherwood, Hawkins Co., Tenn.

Type locality: Falls of the Ohio.

22. PLETHOBASUS CYPHYUS COMPERTUS (Frierson), 1911.

Unio varicosus Lewis, '71.—*Unio compertus* Frierson, '11, p. 53, pl. 3 (middle and lower figures).—*Pleurobema compertum* Simpson, '14, p. 809.

Specimens in the Walker collection from "Holston River, Knoxville," are authentically labeled *varicosus* Lewis, and *compertus* Frierson, and they agree very well with specimens collected by myself in French Broad River, at Boyd Creek, Sevier Co., Tenn. My specimens (I have five) are larger than Frierson's figures, and most of them are more drawn out posteriorly. They were found associated with one specimen of the true *P. cyphus*, and resemble the latter very much, except that the radial row of knobs on the disk is poorly developed, almost obliterated, and that the soft parts are not of orange, but of pale color. (For the rest, the anatomy of male and female is like that of *P. cyphus*.)

I consider this as a variety of *P. cyphus*, since in some of my specimens, the row of knobs is more distinct, and since typical

cyphus often has these knobs nearly obliterated. Whether the soft parts are always pale remains to be seen (the specimen of typical *cyphus* from the same locality had orange soft parts): but several other shells have, in the French Broad, the tendency to develop pale soft parts, or pale nacre, while they are tinted elsewhere.

This seems to be a rare shell, which has been reported by Lewis from the Tennessee below Knoxville, by Frierson from the "Clinch and Holston"; Walker has specimens from "Holston, Knoxville" (probably Tennessee), and I found it in the lower French Broad. It might be that this is a local race, restricted in its distribution, and possibly with its center in the lower French Broad: but more material with exact localities should be secured.

Type locality: Clinch and Holston rivers.

Genus: LEXINGTONIA Ortmann (1914).

Ortmann, 1914, p. 28.

23. LEXINGTONIA DOLABELLOIDES (Lea), 1840.

Unio dolabelloides Lea, '40.—*Unio thorntoni* Lea, '57.—*Unio mooresianus* Lea, '57.—*Unio recurvatus* Lea, '71.—*Unio circumactus* Lea, '71.—*Unio subglobatus* Lea, '71.—*Unio dolabelloides* and *mooresianus* Lewis, '71.—*Pleurobema dolabelloides* Simpson, '14, p. 752.

U. thorntoni, *mooresianus*, *recurvatus*, *circumactus*, and *subglobatus* have been recognized by Simpson as synonyms of this.

Also here we have a case where a swollen form (*dolabelloides*) is found in the larger rivers, and a compressed one (*conradi*) in the smaller streams, with the intergrades existing between them. I have drawn the line between the two at the diameter of 50 per cent. of the length, so that forms with the diameter 50 per cent. or over are *dolabelloides*, and those below 50 per cent. are *conradi*.

L. dolabelloides in its typical development is a swollen form, generally also with more elevated beaks. It is known from the Tennessee River below Knoxville (Lewis), down to Rathburn, Hamilton Co. (Walker collection), and from the lower Clinch, up to Agee, Campbell Co. (where it intergrades with *conradi*); and it is in French Broad River, at Boyd Creek, Sevier Co.

It is remarkable that this form has not been found in the Holston proper, from Knoxville up to the forks, while the headwaters-form is both in the North and South Fork Holston.

Type locality: "Holston River, Tennessee," which stands apparently for Tennessee River.

24. LEXINGTONIA DOLABELLOIDES CONRADI (Vanatta), 1915.

Unio maculatus Conrad, '35.—*Pleurobema maculatum* Goodrich, '13, p. 94.—*Pleurobema maculatum* Simpson, '14, p. 737.—*Pleurobema appressum* Simpson, '14, p. 747.—*Pleurobema conradi* Vanatta, '15, p. 559.

A form, largely misunderstood. Specimens of this have often been called *U. appressus* Lea, because two specimens are in the U. S. Nat. Mus. with the figured type of *appressus*, but are different from the latter. Also Simpson's *P. appressum* ('14, p. 747) undoubtedly is this, since he quotes Sowerby's figure of *U. argenteus* (Conch. icon. 16. Unio. '66, pl. 37, f. 204), which is a fine representation of this form.

This variety often resembles very much *Pleurobema oviforme* (Conr.) (chiefly such forms which have been called *clinchense* Lea). However, it may be recognized by the subtriangular outline, more forwardly inclined beaks, and the more distinct truncation of the posterior slope. The most important character, however, is seen in the soft parts: in the present form, these are generally deep orange, with the outer gills marsupial, filled, when charged, with *red, subcylindrical* placentæ. These are the characters of the genus *Lexingtonia*. The main species has the same characters, at least in the Clinch; in the French Broad, however, I have found specimens with pale soft parts. But the same tendency has been noticed in other species from the French Broad.

An abundant form in the headwaters of Powell, Clinch, North and South Fork Holston. In the Powell, it goes up to Big Stone Gap, Wise Co., Va., and is also in Puckell Creek at Pennington Gap, Lee Co., Va. In the Clinch, it is found up to Cedar Bluff, Tazewell Co., Va., and down to Clinton, Anderson Co., Tenn., intergrading in the lower part with typical *dolabelloides*. It is everywhere in the

North Fork Holston up to Saltville, Smyth Co., Va., and in the South Fork Holston at Fish Dam (Walker coll.), Emmett, and Bluff City, Sullivan Co., Tenn. However, it does not go down the Holston proper (see above).

Type locality: (of *U. maculatus* Conr.) Elk and Flint rivers, northern Alabama (Conrad's Flint River is in Morgan Co., Ala., and is different from the Flint River in Madison Co., Ala.).

Note: This group of forms is also abundant in the Tennessee drainage in northern Alabama. The typical *dolabelloides* is found in the Tennessee proper, and also in lower Paint Rock River, Flint River (Madison Co.), and Limestone Creek; while the *conradi*-type is found in smaller streams, for instance, in the headwaters of Paint Rock River, the headwaters of Flint River (Madison Co.), Flint River (Morgan Co., according to Conrad), and in Elk River (Conrad).

Genus: PLEUROBEMA Rafinesque (1820).

Ortmann, 1912b, p. 261.

25. PLEUROBEMA OBLIQUUM (Lamarck), 1819.

Unio obliqua Lamarck, '19.—*Unio obliquus* Pilsbry & Rhoads, '96.—*Pleurobema obliquum* Ortmann, '12b, p. 264 (anatomy).—*Quadrula obliqua* Simpson, '14, p. 881.

This consists of a group of forms very variable in shape, which has been divided into a number of "species." In the upper Tennessee region several of the latter are found, but they all intergrade with each other, and there is very little indication of their separation into geographical or ecological races. Mostly, the various forms are found associated, so that they are hardly more than individual variations.

However, in deference to the nomenclature hitherto accepted, and in view of the fact that in other regions some of these variations become local varieties, I have kept these forms apart.

The typical *P. obliquum* is rather upright, with a distinct radial furrow, and is subtriangular in outline. The nacre is generally white.

This form is quite abundant in the larger rivers, Tennessee,

Clinch, Holston, and French Broad. It goes up, in the Clinch, to Union Co., Tenn.; in the Holston, to Grainger Co., Tenn. In the Tennessee proper it is known down to Chattanooga. It is rather strange that it is absent in Lewis's list.

In specimens from the upper section of Holston and Clinch, the radial furrow is quite shallow.

Type locality: Ohio River.

26. *PLEUROBEMA OBLIQUUM CORDATUM* (Rafinesque), 1820.

Obovaria cordata Rafinesque, '20.—*Unio plenus* Lea, '40.—*Unio plenus* Lewis, '71.—*Quadrula plena* Simpson, '14, p. 886.—*Quadrula cordata* Vanatta, '15, p. 558.—*Pleurobema obliquum plenum* Utterback, '16, p. 77.

I accept the nomenclatural change introduced by Vanatta, since Rafinesque's description and figure can very well be referred to this form.

Upright, more rounded, and more elevated than the normal form, radial furrow less developed.

This is the most poorly marked form of the group, and is found with the main form all over its range, representing merely an individual variation. In the upper Tennessee region it is rather scarce.

Type locality: Ohio River.

27. *PLEUROBEMA OBLIQUUM CATILLUS* (Conrad), 1836.

Unio catillus Conrad, '36.—*Unio solidus* Lea, '38.—*Quadrula solida* Simpson, '14, p. 885.—*Pleurobema obliquum catillus* Utterback, '16, p. 79.

Subtriangular, rather swollen, with the radial furrow obliterated or absent. Nacre white or reddish.

Individual variation of the main form, all over its range, but quite rare in the upper Tennessee; there are mighty few specimens which show the characters of this form well developed.

In other regions (upper Ohio, and west of the Mississippi) this form assumes frequently the character of a local race, in fact, west of the Mississippi, this, and forms like *P. obliquum rubrum*, prevail,

while the form *coccineum* is scarce, and the typical *obliquum* is absent.

Type locality: Scioto River, Ohio.

28. PLEUROBEMA OBLIQUUM COCCINEUM (Conrad), 1836.

Unio coccineus Conrad, '36.—*Pleurobema coccineum* Ortmann, '12b, p. 263 (anatomy).—*Pleurobema* sp. ? Goodrich, '13, p. 94.—*Quadrula coccinea* Simpson, '14, p. 883.

A compressed form, typically merely a compressed *catillus*, with the radial furrow absent.

Such forms have been reported hitherto only once from the upper Tennessee by Call (from "Holston River"). I have found only a few of them, corresponding entirely to the *coccineum* of the upper Ohio drainage in Pennsylvania; in the Clinch at Solway, Knox Co., Tenn., and in the Holston at Hodges, Jefferson Co., and at Noeton, Grainger Co., Tenn. They stand very close to the *catillus* forms of this region, representing merely an individual variation of it.

Type locality: Mahoning River, near Pittsburgh (=Mahoning River, Lawrence Co., Pa.).

In addition to the above form, there is, in the upper Clinch, a very peculiar form of this group, not found elsewhere, which may be described as a compressed *obliquum*, with traces of the radial furrow still present. I have seen the soft parts of this (including a gravid female), so that there is no doubt about the affinities of this shell. This form requires further study, and might deserve a varietal name, for it is found, in the Clinch, at, and a good deal above, the upper limit of *P. obliquum*.

In the Walker collection there are several such specimens from Needham's Ford, Union Co., Tenn., and I have it from Clinchport, Scott Co., Va., and from Cleveland, Russell Co., Va.

This form may be more abundant in the poorly known portion of the Clinch from Claiborne and Grainger Cos., through Hancock Co., Tenn., to the Virginia state line.

29. PLEUROBEMA OBLIQUUM RUBRUM (Rafinesque), 1820.

Obliquaria rubra Rafinesque, '20.—*Unio pyramidatus* Lea, '34.—*Unio mytiloides* Lewis, '71.—*Unio pyramidatus* Pilsbry & Rhoads, '96.—*Pleurobema pyramidatum* Ortmann, '12b, p. 264 (anatomy).—*Quadrula pyramidata* Simpson, '14, p. 888.—*Quadrula rubra* Vanatta, '15, p. 557.

According to Vanatta, the type of *Obliquaria rubra* Raf. is the same as *U. pyramidatus* of Lea. Since already Conrad ('34 and '36) has brought *rubra* together with *pyramidatus* Lea and his own *mytiloides* (which is *pyramidatus*), this nomenclatural change should be accepted.

Shell oblique, with high, forwardly inclined beaks. Radial furrow more or less developed. Nacre generally red.

Although, in its typical phase, quite distinct from normal *obliquum*, intergrades do exist, and also intergrades toward *cordatum* and *catillus* have been observed.

Also this form generally accompanies *P. obliquum*, but both in Clinch and Holston it ascends the rivers a little farther. In the Clinch, it goes to Oakman, Grainger Co., Tenn., and in the Holston to Austin Mill, Hawkins Co., Tenn. It is abundant and well developed in this region, and of all the forms of the *obliquum* group, it has the best claim to be regarded as a local race.

In the upper Ohio, this form is quite rare, and often not typical. West of the Mississippi are peculiar forms of it, often with the radial furrow quite obliterated.

Type locality: Kentucky River.

GROUP OF PLEUROBEMA OVIFORME.

Also here we meet with a group in which the rule holds good that flat forms of the headwaters are represented, farther down stream, by more swollen forms.

Generally speaking, the *oviforme* group represents, in the upper Tennessee, the *P. clava* of the Ohio drainage, but it is much more variable, and has developed, in the headwaters, a very peculiar, compressed type, which does not find a parallel in the upper Ohio system. All these forms have the characteristic *Pleurobema* anatomy, and

resemble very much in this the *P. clava*, although some peculiar variations are observed in the color of certain parts.

As it happens, the oldest name (*oviforme*) has been used for an intermediate form, and thus, in order to retain this in its original sense, it seems advisable to distinguish *three* types within this species: the headwaters form (*argenteum*) has a diameter of less than 40 per cent. of the length; the form of the medium sized rivers (*oviforme*) has a diameter from 40 to 49 per cent.; and the big river form (*holstonense*) has 50 per cent and over.

Also here we see the phenomenon that the headwaters form gains in circumference what it has lost in obesity. The *argenteum* type shows this possibly to the greatest extent; shells of this form reach in length and height dimensions entirely unknown in the more swollen forms.

30. PLEUROBEMA OVIFORME (Conrad), 1834.

Unio oviformis Conrad, '34.—*Unio ravenelianus* Lea, '34.—*Unio patulus* Conrad, '38 (not *patulus* Lea, '29).—*Unio lesleyi* Lea, '60.—*Unio ornatus* Lea, '61.—*Unio clinchensis* Lea, '67.—*Unio conasaugaensis* Lea, '72.—*Unio clinchensis, lesleyi, patulus* Lewis, '71.—*Pleurobema oviforme* Goodrich, '13, p. 94.—*Pleurobema clinchense, lesleyi, oviforme, ornatum, conasaugaense, ravenelianum* Simpson, '14, pp. 743–800.

This resembles much the upper Ohio form of *P. clava*, but is less cuneate, with the beaks less anterior. It is extremely variable in shape, higher or more elongate, and the color pattern is hardly ever alike in any two individuals.

In the Walker collection are topotypes of *U. ravenelianus* Lea (from Asheville): six specimens have the diameter of *oviforme* (40–49 per cent., while one has the diameter of 38 per cent. and the latter would thus fall under *argenteum*. But it has the typical shape of *oviforme*. Since the type of *ravenelianus* has 43 per cent., according to Simpson, we should place this here, and these shells are, indeed, nothing but *oviforme* without rays, of a general dull color (pale brownish, not yellowish). Such specimens are found elsewhere, and several sets in the Walker collection, from Poplar Creek,

Roan Co., from the Little Tennessee, Monroe Co., and Cane Creek, McMinn Co., are labeled *ravenelianus*. I have found similar ones in Hiwassee River (passing into *holstonense*). I do not think that these are more than individual variations. However, it might be that within the high mountains of North Carolina, *P. oviforme* generally assumes these characters (dull color and lack of rays), and if so, we might be justified in calling this form by a varietal name (*P. oviforme ravenelianum*).

The figure of *U. conasaugaensis* Lea is an *oviforme* according to diameter, but is an *argenteum* according to shape and size. Since topotypes and authentic material of *conasaugaensis*, examined in the Walker collection, fall partly under *oviforme* and partly under *argenteum*, this is a real intergrade, hard to place.

P. oviforme is widely distributed in all rivers in East Tennessee. In the Tennessee proper it is rare, and is generally represented by the var. *holstonense*. It is in Powell, Clinch, Holston, French Broad, Little Tennessee, and in many of their tributaries, passing in the lower parts of the larger rivers into *oviforme holstonense*, and in the upper parts into *oviforme argenteum*. It is to be noted that *oviforme* goes well into the headwaters, and apparently it does not pass into *argenteum* in some instances. This is chiefly the case in French Broad River, where it goes into the North Carolina mountains (Asheville) without assuming the characteristic features of *argenteum*.

Type locality: Tennessee.

31. PLEUROBEMA OVIFORME ARGENTEUM (Lea), 1841.

Unio argenteus Lea, '41.—*Unio striatissimus* Anthony, Am. Jl. Conch., 1, '65, p. 155.—*Unio planior* Lea, '68.—*Unio brevis* Lea, '72.—*Unio argenteus* Lewis, '72.—*Unio swordianus* Wright, Naut., 11, '97, p. 4.—*Pleurobema fassinans* Ortmann, '13b, p. 310 (not *fassinans* of Lea).—*Pleurobema argenteum* Goodrich, '13, p. 94.—*Pleurobema swordianum*, *argenteum*, *breve*, *planius* Simpson, '14, pp. 757–802.—*Pleurobema fassinans* Ortmann, '14, p. 31 (per errorem).

The soft parts of this form have been described by me under the erroneous name of *P. fassinans*.

Simpson (p. 804) makes *U. striatissimus* Anthony a synonym of *P. estabrookianum* (which actually is *Fusconaia barnesiana bigbyensis*). Specimens from Blount Co., Tenn., received from the Alabama Museum of Nat. Hist. as *striatissimus*, and similar ones with the same label in the Walker collection, agree fully with specimens collected by myself in Little River in Blount Co., and are this form.

Walker has four specimens labeled *P. swordianum* (Wright) from the Wright collection, which thus are authentic specimens. They are all typical *P. oviforme argenteum*. In addition, he has three others from the Sword collection (original lot), of which two are this form, while the third is *Fusconaia pilaris bursa-pastoris*. The type of *swordianum* has, according to Simpson, the diameter of 40 per cent., and thus would stand under *oviforme*. This, however, seems to be an extreme specimen.

This is the compressed form of *oviforme*, peculiar to the headwaters and other small streams. It also generally attains a larger size than the typical *oviforme*, and is more rhomboidal in outline. Lea's only type of *U. argenteus* (examined by myself in Washington) is not a normal specimen; it is tapering behind, which is a character of *oviforme*. *U. planior* represents the normal shape of this shell, rhomboidal, while *U. brevis* is exactly the same thing, only slightly shorter. The color markings are generally less bright than in *oviforme*, and very often they are obscure or missing, chiefly in old shells.

This variety is found in Powell River from Big Stone Gap, Wise Co., Va. (where it alone is present), downward (associated with *oviforme*); in the Clinch, from Tazewell Co., Va., down to Kyle Ford, Hancock Co., Tenn. (also associated with *oviforme* and intergrading with it). In the Holston drainage it is pure in Big Mocassin Creek, and in the North Fork at Saltville, Smyth Co., and Holston, Washington Co., Va. It is also pure in the Middle Fork at Chilhowie, Smyth Co., in the South Fork at Barron, Washington Co., Va., and in Watauga River at Watauga, Carter Co., Tenn. Farther down, it passes into, and is associated with, *oviforme*, but has not been found in the Holston proper. It is in Little Pigeon River, at Sevierville, Sevier Co., Tenn., but not very well developed here, the

majority of the specimens belonging to *oviforme*. In Little River, at Walland and Melrose, Blount Co., Tenn., it is well developed, pure, and not accompanied by *oviforme*. The Little River form has been called *striatissimus*, and it has one peculiarity in the soft parts; they are of the orange type, and the placentæ are red. *P. oviforme argenteum* is also in the tributaries of Hiwassee River (in Conasauga Creek with *oviforme*), and in South Chickamauga Creek, at Ringgold, Catoosa Co., Ga. The latter specimens have, in the average, a greater diameter, resembling that of *oviforme*, but they are stunted in growth (truncated behind). A few of normal shape are clearly *argenteum*. In the larger rivers, this form is missing.

Type locality: Holston River, Tenn. (not recently found in Holston proper).

32. PLEUROBEMA OVIFORME HOLSTONENSE (Lea), 1840.

Unio holstonensis Lea, '40.—*Unio mundus* Lea, '57.—*Unio tesserulæ* Lea, '61.—*Unio pattinoides* Lea, '71.—*Unio acuens* Lea, '71.—*Unio lawi* Lea, '71.—*Unio holstonensis* and *tesserulæ* Lewis, '71.—*Unio bellulus* Lea, '72.—*Unio acuens* and *lawi* Pilsbry & Rhoads, '96.—*Pluerobema holstonense*, *acuens*, and *tesserulæ* Simpson, '14, pp. 739, 746, 749.

U. mundus, *lawi*, *pattinoides*, and *bellulus* have already been recognized by Simpson as synonyms of *P. holstonense*.

This is the swollen, large river form, of *oviforme*. *U. holstonensis*, *pattinoides*, *acuens*, and *lawi* are less swollen than the others (*mundus*, *tesserulæ*, *bellulus*), but they all pass gradually into each other with regard to obesity.

This form has been reported from the Tennessee below Knoxville, and down to the mussel shoals in northern Alabama; and further from the lower Clinch, the lower Emory River, and the Noli-chucky. According to the material examined by the writer, it goes up, in the Clinch, to Edgemoor, Anderson Co., Tenn.; in the Holston, to Mascot, Knox Co., Tenn.; it is in French Broad at Boyd Creek, Sevier Co., Tenn.; in Little Tennessee River, Monroe Co., Tenn. (Walker coll.); and in the Hiwassee at Austral, Polk Co., Tenn. At all these points, near its upper limit, it is associated and intergrades with *oviforme*.

Type locality: Holston River, Tenn. (Simpson says: Tusculumbia, Ala.) (topotypes examined).

Note: The group of *Pleurobema oviforme* is also quite abundant in the Tennessee drainage in North Alabama. Also here the *holstonense*-form is in the Tennessee proper (also in lower part of Paint Rock River and Limestone Creek); in the tributaries, *oviforme* is the prevailing form, and in some of the headwaters, the *argenteum*-form is fully as well developed as in the upper Clinch and Holston, for instance: in Paint Rock River at Princeton, Jackson Co., Ala.; Dry Creek, Holly Tree, Jackson Co., Ala. (tributary to Paint Rock); in Hurricane Creek, Gurley, Madison Co., Ala. (tributary to Flint River); in Elk River, Estill Springs, Franklin Co., Tenn., and its tributary: Boiling River, Cowan, Franklin Co., Tenn.

It should be remarked that in this region also the true *Pleurobema clava* (Lam.) turns up; this species is distinguished by much more anteriorly situated, pointed beaks, swollen anterior part of the shell, and cuneiformly compressed posterior part. The Carnegie Museum has this species from the old Smith collection, labeled Tusculumbia, Ala., and I have seen it also in the Walker coll. from Florence, Ala. In addition, in the latter collection, are specimens from Sequatchie River, at Jasper, Marion Co., Tenn. (Wetherby coll.).

Genus: ELLIPTIO Rafinesque (1820).

Ortmann, 1912b, p. 265.

33. ELLIPTIO NIGER (Rafinesque), 1820.

Unio nigra Rafinesque, '20.—*Unio crassidens* Lewis, '71.—*Unio crassidens* Pilsbry & Rhoads, '96.—*Elliptio crassidens* Ortmann, '12b, p. 266 (anatomy).—*Unio crassidens* Simpson, '14, p. 606.—*Unio crassidens* Vanatta, '15, p. 555.—*Elliptio nigra*, Utterback, '16, p. 88.

The identity of *U. nigra* Raf. is now firmly established (Say, Conrad, Kuester, Sowerby, and Vanatta), and it is the species commonly called *crassidens*. However, the type of *crassidens* Lamarck, 1819, is not this, but is the *trapezoides* Lea (Frierson, '14a, p. 7). Thus Rafinesque's name should be used for the present species.

Everywhere in the larger rivers: Tennessee, Holston, French Broad, Clinch, and Powell; goes up, in the Powell, to Jonesville, Lee Co., Va.; in the Clinch, to Clinchport, Scott Co., Va.; in the Holston to the South Fork at Pactolus, Sullivan Co., Tenn.; in the French Broad, it goes to the Nolichucky at its mouth (Chunn's Shoals, Hamblen Co., Tenn.). It is also in Emory River, up to Harriman Junction, Roan Co., Tenn., and in Hiwassee River, at Kincannon Ferry, Meigs Co., Tenn. In the Tennessee below Knoxville, and down to Chattanooga, it is extremely abundant.

Type locality: Ohio River.

34. *ELLIPTIO DILATATUS* (Rafinesque), 1820.

Unio dilatatus Rafinesque, '20.—*Unio gibbosus* Lewis, '71.—*Unio gibbosus* Pilsbry & Rhoads, '96.—*Elliptio gibbosus* Ortmann, '12b, p. 271 (anatomy).—*Elliptio dilatatus* Ortmann, '13b, p. 311.—*Elliptio gibbosus* Goodrich, '13, p. 94.—*Unio gibbosus* Simpson, '14, p. 597.—*Unio dilatatus* Vanatta, '15, p. 555.—*Elliptio dilatata* Utterback, '16, p. 90.

Common, in large rivers as well as in small creeks, possibly the most widely distributed species in the upper Tennessee region, so that it is hardly required to name special localities. However, it should be mentioned that it is one of the species which go up, in French Broad River, to Asheville, Buncombe Co., N. Car. (Walker coll.).

In our region, this species is of moderate size, and purple color of the nacre prevails; only specimens from the French Broad are more frequently white-nacred.

Type locality: Ohio River (the type is from Kentucky River, according to Vanatta).

Genus: *LASTENA* Rafinesque (1820).

Ortmann, '12b, p. 297, and '15, p. 106.

35. *LASTENA LATA* (Rafinesque), 1820.

Anodonta lata Rafinesque, '20.—*Margaritana dehiscens* Lewis, '71.—*Lastena lata* Goodrich, '13, p. 94.—*Lastena lata* Ortmann, '15, p. 106 (anatomy).—*Lastena lata* Vanatta, '15, p. 554.

Reported from Tennessee River, below Knoxville (Lewis), and the Holston River (Call). I have never found it in the Holston, but only in the Clinch, at Edgemoor and Clinton, Anderson Co., Tenn.; at Oakman, Grainger Co., Tenn. In the Walker collection it is from Clinch River at Clinchport, Scott Co., Va.; and I collected it still farther up at St. Paul, Wise Co., and Cleveland, Russel Co., Va. It is undoubtedly a rare shell.

Type locality: Kentucky River.

Subfamily: ANODONTINÆ Ortmann.

Ortmann, 1910, p. 117.

Genus: LASMIGONA Rafinesque (1831).

Symphynota Lea (1829), Ortmann, '12b, p. 280.—*Lasmigona* Frierson, '14b, p. 40.

36. LASMIGONIA (SULCULARIA) BADIA (Rafinesque), 1831.

Alasmodon badium Rafinesque, '31.—*Margaritana holstonia* Lewis, '71.—*Symphynota holston(ia)* Goodrich, '13, p. 94.—*Alasmidonta holstonia* Simpson, '14, p. 502.—*Symphynota (Sulcularia) badia* Frierson, '14a, p. 7.—*Symphynota (Alasminota) holstonia* Ortmann, '14, p. 43 (anatomy).

The subgenus *Alasminota* Ortmann, '14, p. 42, is synonym to *Sulcularia* Rafinesque, '31; see Frierson, l. c.

A characteristic small stream species, abundant locally, and reported by Lewis from small streams in Monroe Co., Tenn., and by Call from tributaries of the Holston in East Tennessee.

The largest streams where I have seen it are the upper Holston proper at Church Hill, Hawkins Co., Tenn., and the Hiwassee, at Austral, Polk Co., Tenn. In both cases the specimens came from a small slough. In the headwater streams, it is in upper Powell, in Va., in the uppermost Clinch in Tazewell Co., Va.; in Little Mocassin Creek, Scott Co., Va.; South Fork Holston at Bluff City, Sullivan Co., Tenn.; Watauga River, Carter Co., Tenn.

Other small streams are the following: Cove Creek, Campbell Co., Tenn. (to Clinch); Bull Run, Knox Co., Tenn. (to Clinch);

Big Creek, Hawkins Co., Tenn. (to Holston); Long Creek, Cocke Co., Tenn. (to French Broad); Little Pigeon River, Sevier Co., Tenn. (to French Broad); First Creek and Third Creek, Knox Co., Tenn. (to Tennessee); Piney River, Rhea Co., Tenn. (to Tennessee); Conasauga Creek, Monroe Co., Tenn. (to Hiwassee); South Chickamauga Creek, Catoosa Co., Ga. (to Tennessee).

Thus this species has practically a universal distribution in our region, but it strictly avoids larger streams.

Type locality: Small streams of the Knobs, Kentucky (headwaters region of Cumberland and Kentucky Rivers).

37. *LASMIGONA* (*LASMIGONA*) *COSTATA* (Rafinesque), 1820.

Alasmidonta costata Rafinesque, '20.—*Margaritana rugosa* Lewis, '71.—*Alasmodonta rugosa* Pilsbry & Rhoads, '98.—*Symphynota costata* Ortmann, '12b, p. 283 (anatomy).—*Symphynota costata* Ortmann, '13b, p. 311.—*Symphynota costata* Goodrich, '13, p. 94.—*Symphynota* (*Lasmigona*) *costata* Simpson, '14, p. 488.

A common species, most abundant in small and medium-sized streams, rarer in the larger rivers, but not absent there (Tennessee, lower Clinch and Holston). Goes up, in the Powell, to Olinger, Lee Co., Va.; in the Clinch, to Cedar Bluff, Tazewell Co., Va.; it is in Emory River; goes, in North Fork Holston, to Saltville, Smyth Co., Va.; in Middle Fork Holston, to Chilhowie, Smyth Co., Va.; in South Fork Holston, to Barron, Washington Co., Va.; in Watauga, to Johnson City, Washington Co., Tenn. It is also in South Chickamauga Creek, Ringgold, Catoosa Co., Ga.

Type locality: Kentucky River.

Genus: *ANODONTA* Lamarck (1799).

Ortmann, '12b, p. 286.

38. *ANODONTA* *GRANDIS GIGANTEA* (Lea), 1834.

Anodonta gigantea Lea, '34.—*Anodonta grandis* (incl. *gigantea*) Ortmann, '12b, p. 292 (anatomy).—*Anodonta grandis gigantea* Simpson, '14, p. 420.

No *Anodonta* has ever been reported from the upper Tennessee

region. However, in the collection of B. Walker, there are two large specimens of a form of *Anodonta grandis* Say, collected by Mr. M. D. Barber, of Knoxville, in a "small mud pond near French Broad River, 8 miles above Knoxville." The largest has a length of 168 mm., the other of 127 mm. In the latter, the beak sculpture is visible, and corresponds to that of *A. grandis*; it has white nacre, and much resembles specimens of the var. *gigantea* Lea, as found in western Pennsylvania. The other (larger) is a little distorted and tapering behind, and has pale purple nacre, resembling in these characters some of the southern forms of the species.

The occurrence of this form in this isolated locality is quite remarkable, but supports the view that *Anodontas* may possess exceptional means of dispersal. According to more detailed information obtained by Mr. Walker in 1916 from Mr. Barber, the pond is "plainly natural, some 4 or 5 rods long by 2 rods wide, with soft deep mud. There was a small stream of water running to the French Broad River, just a short distance. This was 10 or 11 years ago." "Two years ago, I took a nephew and found the same pond, but although we waded the pond in every direction, up to our knees in mud, we could not find even a fragment of *gigantea*. A man living near there said he had seen large shells in another pond near, but I have not examined it." These ponds, a short distance from the river, probably are on the flood plain of French Broad; the writer has not been able to locate them on the U. S. Geol. Surv. maps.

Type locality: Port Gibson, Claiborne Co., Miss.

Genus: ANODONTOIDES Simpson (1898).

Ortmann, 12b, p. 294.

39. ANODONTOIDES FERUSSACIANUS (Lea), 1834.

Anodonta ferussaciana Lea, '34.—*Anodontoides ferussacianus* Ortmann, '12b, p. 294 (anatomy).—*Anodontoides ferussacianus* Simpson, '14, p. 467.

Anodonta oblita (?) Lewis, '71, may possibly stand for this species. Lewis doubtfully reports this from the Tennessee below Knoxville, but this probably is a mistake. Originally, *A. oblita* Lea

and *Anodonta denigrata* Lea, which are this species, have been described from Campbell Co., Tenn.: this is surely in the Cumberland drainage, since Wilson & Clark report it ('14) from Clear Fork, at Jellico, Campbell Co., Tenn., and other places in the upper Cumberland region in Kentucky (I found it myself in Cumberland River at Orby, Bell Co., Ky.).

In the Walker collection are two specimens from Powell River, Lee Co., Va., collected by G. F. Sword. There is no mistake about them, and thus this species must be listed with the upper Tennessee shells, although known only from a single and somewhat indefinite, locality, and remarkable for its absence all over the rest of this region.

Type locality: Ohio River, Cincinnati, Ohio.

Genus: *ALASMIDONTA* Say (1818).

Ortmann, '12b, p. 294.

40. *ALASMIDONTA (PRESSODONTA) MINOR* (Lea), 1845.

Margaritana minor Lea, '45.—*Margaritana minor* Lewis, '72.—*Alasmidonta (Pressodonta) minor* Ortmann, '12b, p. 295.—'14, p. 46 (anatomy).—*Alasmidonta minor* Ortmann, '13b, p. 311.—*Alasmidonta minor* Goodrich, '13, p. 94.—*Alasmidonta (Pressodonta) minor* Simpson, '14, p. 498.

A characteristic small creek species, locally abundant. It is found all over the region, but strictly avoids the medium-sized and larger rivers. I have never seen it in the Clinch South of the Va.-Tenn. state line, and never in the Holston proper. I know it from the following stations.

South Fork Powell River, Big Stone Gap, Wise Co., Va.; North Fork Clinch River, Tazewell, Tazewell Co., Va. (Walker coll.); Clinch River, Cedar Bluff, and Richland, Tazewell Co., Va.; Clinch River, Cleveland, Russell Co., Va.; Clinch River, St. Paul, Wise Co., Va.; Clinch River, Speers Ferry, Scott Co., Va.; Brush Fork (tributary to Poplar Creek and Clinch), Marlow, Anderson Co., Tenn.; Big Mocassin Creek, Mocassin Gap, Scott Co., Va.; North Fork Holston River, Saltville, Smyth Co., Va.; Middle Fork Holston River,

Chilhowie, Smyth Co., Va.; South Fork Holston River, Barron, Washington Co., Va.; Big Creek (tributary to Holston), Rogerville, Hawkins Co., Tenn. (Walker coll.); Little Pigeon River, Sevierville, Sevier Co., Tenn.; Boyd Creek, Boyd Creek, Sevier Co., Tenn.; Little River, Melrose, Blount Co., Tenn.; Pistol Creek, Rockford, Blount Co., Tenn.; Conasauga Creek, Monroe Co., Tenn. (Walker coll.); South Chickamauga Creek, Ringgold, Catoosa Co., Ga.

Type locality: Tennessee (and "North Carolina," but no exact locality given).

41. *ALASMODONTA* (*DECURAMBIS*) *MARGINATA* (Say), 1819.

Alasmodonta marginata Say, '19.—*Margaritana marginata* Lewis, '71.—*Alasmodonta marginata* Pilsbry & Rhoads, '96.—*Alasmodonta marginata* Ortmann, '12b, p. 297 (anatomy).—*Alasmodonta marginata* Ortmann, '13b, p. 311.—*Alasmodonta marginata* Goodrich, '13, p. 94.—*Alasmodonta* (*Rugifera*) *marginata* Simpson, '14, p. 504.

As to the subgenus *Decurambis* Raf., '31, see Frierson, '14a, p. 7.

Generally distributed over the whole upper Tennessee region, but apparently more abundant toward the headwaters. Goes, in the Powell, to Olinger, Lee Co., Va.; in the Clinch, to Richland, Tazewell Co., Va.; in the Forks of the Holston, to Saltville and Chilhowie, Smyth Co., Va., and is also in Big Mocassin Creek, Scott Co., Va. Pilsbry & Rhoads report it from Watauga River at Johnson City, Washington Co., Tenn. It is also in Ocoee River, at Ducktown, Polk Co., Tenn. (Walker coll.).

Type locality: Scioto River, Chillicothe, Ohio.

42. *ALASMODONTA* (*DECURAMBIS*) *RAVENELIANA** (Lea), 1834.

Margaritana raveneliana Lea, '34.—*Alasmodonta* (*Rugifera*) *raveneliana* Simpson, '14, p. 507.

Differs from *A. marginata* chiefly in the absence of rugosities on the posterior slope. However, in very young specimens, traces of them are sometimes seen, so that this characteristic feature of the subgenus *Decurambis* (*Rugifera*) is still indicated. This form undoubtedly is an offshoot of the *marginata*-stock, separated from the

rest in the high mountains of North Carolina, and developed there into a good species.

The type locality is French Broad and Swananoa rivers, Asheville, Buncombe Co., N. Car. I have not been able to find this species there, for the French Broad is polluted in this region (lumber industries on Davidson River). But I have rediscovered it in Big Pigeon River, at Canton, Haywood Co., N. Car., where it is not rare at the proper places.

Specimens from "North and South Fork of the Cumberland River," referred to this species, do not belong here, but are a form of *A. marginata*, with well-developed rugosities upon the posterior slope (*atropurpurea* Raf., '31).

Genus: PEGIAS Simpson (1900).

Ortmann, '14, pp. 45 and 65 (as subgenus).

On account of the very peculiar glochidia I consider it better to retain *Pegias* as a genus, closely allied to *Alasmidonta*.

43. PEGIAS FABULA (Lea), 1836.

Margarita (Margaritana) fabula Lea, '36.—*Alasmidonta fabula* Ortmann, '13b, p. 311.—*Alasmidonta (Pegias) fabula* Ortmann, '14, p. 65 (anatomy).—*Pegias fabula* Simpson, '14, p. 473.

A rare species in the upper Tennessee drainage, apparently preferring smaller streams. Possibly it has been often overlooked on account of its small size and the peculiarity of being generally much eroded. I know it from the following localities.

Wallen Creek, Lee Co., Va. (Walker coll.); Powell River, Dryden, Lee Co., Va.; Big Mocassin Creek, Mocassin Gap, Scott Co., Va.; North Fork Holston River, Saltville, Smyth Co., Va.; North Fork Holston River, Holston, Washington Co. (Walker coll.) and Mendota, Washington Co., Va.; South Fork Holston River, Pactolus, Sullivan Co., Tenn.

Type locality: Cumberland River, Tenn.

Genus: STROPHITUS Rafinesque (1820).

Ortmann, '12b, p. 299.

44. STROPHITUS EDENTULUS (Say), 1829.

Alasmodonta edentula Say, '29.—*Anodonta edentula* Lewis, '72.—*Alasmodonta edentula* Pilsbry & Rhoads, '96.—*Strophitus edentulus* Ortmann, '12b, p. 299 (anatomy).—*Strophitus edentulus* Ortmann, '13b, p. 311.—*Strophitus edentulus* Goodrich, '13, p. 94.—*Strophitus edentulus* Simpson, '14, p. 345.

Walker thinks that the upper Tennessee-form might be distinguished from the normal *edentulus* as var. *shaefferianus* (Lea). He believes that the latter is more compressed and more projecting anteriorly, and has more frequently reddish nacre. In the average, this appears to be correct, yet there are many specimens in my rich material which do not exhibit these characters, and cannot be distinguished from specimens of the normal *edentulus*, as found, for instance, in western Pennsylvania. Thus I do not think it advisable to separate the two forms.

This species is abundant, both in larger rivers and smaller streams: in the Tennessee, in the lower French Board, the Holston and its forks and tributaries, and all over the Clinch and Powell drainages. It goes up, in the Powell, to Big Stone Gap, Wise Co., Va.; in the Clinch to Cedar Bluff, Tazewell Co., Va.; in the Forks of the Holston, to Saltville, Smyth Co., Va., and Bluff City, Sullivan Co., Tenn.

It has not been found by myself in the eastern tributaries of the Tennessee south of the French Broad, but possibly this is accidental.

Type locality: Wabash River.

Subfamily: LAMPSILINÆ Ortmann, 1910.

Ortmann, '10, p. 118.

Genus: ELLIPSARIA Rafinesque (1820).

Ptychobranchnus Simpson, '00.—Ortmann, 12b, p. 305.—*Ellipsaria* Frierson, '14a, p. 7.

45. ELLIPSARIA FASCIOLARIS (Rafinesque), 1820.

Obliquaria fasciolaris Rafinesque, '20.—*Unio phaseolus* Lewis, '71.—*Unio phaseolus* Pilsbry & Rhoads, '96.—*Ptychobranchnus*

phaseolus Ortmann, '12b, p. 306 (anatomy).—*Ptychobranchnus phaseolus* Goodrich, '13, p. 94.—*Ptychobranchnus phaseolus* Simpson, '14, p. 333.—*Ellipsaria fasciolaris* Frierson, '14a, p. 7.—*Ptychobranchnus fasciolaris* Vanatta, '15, p. 554.

Widely and uniformly distributed over the upper Tennessee region, but nowhere in great numbers. In the Tennessee, French Broad, Holston, Clinch, lower Emory, and Powell. It goes up, in the Powell, to Pennington Gap, Lee Co., Va.; in the Clinch, to Cleveland, Russell Co., Va.; in North Fork Holston, to Mendota, Washington Co., Va.; in South Fork Holston, to Emmett, Sullivan Co., Tenn. It is one of the species which has been reported from French Broad River, at Asheville, Buncombe Co., N. Car. It has not yet been found in Little River, Little Tennessee, and Hiwassee, but it is in South Chickamauga Creek, at Ringgold, Catoosa Co., Ga.

Type locality: "Ohio, Wabash, Kentucky rivers." (The type is from Kentucky River, according to Vanatta.)

46. ELLIPSARIA SUBTENTA (Say), 1825.

Unio subtentus Say, '25.—*Unio subtentus* Lewis, '71.—*Unio subtentus* Pilsbry & Rhoads, '96.—*Ptychobranchnus subtentus* Ortmann, '12b, p. 308 (anatomy).—*Ptychobranchnus subtentus* Ortmann, '13b, p. 311.—*Ptychobranchnus subtentus* Goodrich, '13, p. 94.—*Ptychobranchnus subtentum* Simpson, '14, p. 339.

Known from Tennessee, Powell, Clinch, Holston, and Nolichucky rivers, but more abundant toward the headwaters, and rather rare in the big rivers. Goes up to Big Stone Gap, Wise Co., Va.; to Cedar Bluff, Tazewell Co., Va.; and to Smyth Co., Va. (in North and Middle Fork Holston). Also in Big Mocassin Creek, in Scott Co., Va. Thus it ascends, in the small streams, farther than *E. fasciolaris*. In the headwaters it is locally quite abundant.

Type locality: North Fork Holston River (Say says in South Carolina, but this is in Virginia) (topotypes examined).

Genus: OBLIQUARIA Rafinesque (1820).

Ortmann, '12b, p. 309.

47. OBLIQUARIA REFLEXA Rafinesque (1820).

Obliquaria reflexa Rafinesque, '20.—*Unio cornutus* Lewis, '71.—*Unio cornutus* Pilsbry & Rhoads, '96.—*Obliquaria reflexa* Ortmann, '12b, p. 310 (anatomy).—*Obliquaria reflexa* Simpson, '14, p. 330.

Only in the larger rivers. Tennessee below Knoxville (Lewis), and at Rathburn, Hamilton Co., Tenn. (Walker coll.). Lower Clinch, Patton's Ferry, Roan Co., Tenn. (Pilsbry & Rhoads). I found it in the Clinch at Solway, Knox Co.; Edgemoor and Clinton, Anderson Co., Tenn. In the Walker coll. is a specimen from below Agee, Campbell Co., Tenn.

Type locality: Kentucky River and Letart Falls (according to Vanatta, the types are from the latter place, below Parkersburg, W. Va.).

Genus: CYPROGENIA Agassiz (1852).

Ortmann, '12b, p. 312.

48. CYPROGENIA STEGARIA (Rafinesque), 1820.

Obovaria stegaria Rafinesque, '20.—*Unio irroratus* Lewis, '71.—*Unio irroratus* Pilsbry & Rhoads, '96.—*Cyprogenia irrorata* Ortmann, '12b, p. 312 (anatomy).—*Cyprogenia irrorata* Simpson, '14, p. 326.—*Cyprogenia stegaria* Vanatta, '15, p. 554.

Known from the Tennessee below Knoxville (Lewis), and the Holston, at Boyd Island, Knox Co. (Pilsbry and Rhoads). It is also in the Tennessee at Rathburn, Hamilton Co., Tenn. (Walker collection). I traced it up, in the Holston, to Turley Mill, Grainger Co., Tenn.; and in the lower Clinch it is quite abundant, going up to Oakman, Grainger Co., Tenn.

Type locality: Ohio River.

Genus: DROMUS Simpson (1900).

Ortmann, '12b, p. 314.

49. *DROMUS DROMAS* (Lea), 1834.

Unio dromas Lea, '34.—*Unio dromas* Lewis, '71.—*Unio dromas* Pilsbry & Rhoads, '96.—*Dromus dromas* Ortmann, '12b, p. 315 (anatomy).—*Dromus dromas* Simpson, '14, p. 341.

The typical form is rather swollen, and has a large knob or hump on each valve. This knob, however, is very variable.

This form is found in the Tennessee proper. It has been reported by Lewis from below Knoxville, and by Pilsbry and Rhoads from Chattanooga, Hamilton Co. It is in the Walker collection from Chattanooga and from Rathburn, Hamilton Co. Pilsbry and Rhoads report it also from the Holston, at Boyd Island, near Knoxville. I found it only in the Tennessee, three miles below Knoxville.

There are occasional specimens, which might be called by this name, in the lower Clinch and Holston, but in this region it is generally replaced by the next form, with which it intergrades.

Type locality: Harpeth River, Tenn. (and Cumberland River, Nashville, Tenn.).

50. *DROMUS DROMAS CAPERATUS* (Lea), 1845.

Unio caperatus Lea, '45.—*Unio caperatus* Lewis, '71.—*Dromus caperatus* Simpson, '14, p. 343.

This form has lost the "hump," and it is more compressed than the normal form. It begins in the Tennessee at Knoxville (Lewis), and ascends both the Clinch and Holston, where it intergrades, in the lower parts, with typical *D. dromas*. In the Holston, it goes up to Holston Station, Grainger Co., Tenn., and in the Clinch, it goes to Clinch River Station, Claiborne Co., Tenn. It enters also the Powell, and goes up to Shawanee, Claiborne Co., Tenn.

It is quite abundant in the Holston in Knox and Jefferson Cos., although it is frequently associated here with the typical form, and intergrades with it. Its metropolis, however, is in the Clinch from Anderson Co. upward, and in the Powell, where it is a pure race.

Type locality: Clinch River (topotypes examined).

Note: The tendency to develop here a more compressed form in the smaller rivers agrees entirely with the similar phenomenon observed in species of *Fusconaia*, etc.

Genus: OBOVARIA Rafinesque (1820).

Ortmann, 12b, p. 320.

51. OBOVARIA (OBOVARIA) RETUSA (Lamarck), 1819.

Unio retusa Lamarck, '19.—*Obovaria retusa* Ortmann, '12b, p. 321 (anatomy).—*Obovaria (Obovaria) retusa* Simpson, '14, p. 290.

Reported by Call from the Holston River in east Tennessee, but missing in Lewis's list. There are specimens in the Carnegie Museum (from the Smith collection) labeled: Tennessee River, Knox Co., Tenn.; and others in the Walker collection labeled: Holston River, Knox Co., and Holston River, Knoxville, Tenn. In all these cases, apparently, the Tennessee River at and below Knoxville is meant. I found this species only once: a young specimen in Clinch River, at Clinton, Anderson Co., Tenn.

In the Walker collection are also specimens from the Tennessee at Bridgeport, Jackson Co., Ala., and from Florence, Lauderdale Co., Ala. (also reported by Hinkley).

Thus this species seems to belong to the upper Tennessee fauna, going up to Knoxville and into the lower Clinch; but it apparently is very rare.

Some of my specimens of *O. subrotunda* from the Holston (Mascot) have slightly incurved beaks and purple nacre, and resemble *O. retusa* to a degree. Already Wilson and Clark ('14) have indicated a similar approaching of the two species in Cumberland River.

Type locality: ? (Nova Scotia per errorem).

52. OBOVARIA (OBOVARIA) SUBROTUNDA (Rafinesque), 1820.

Obliquaria subrotunda Rafinesque, '20.—*Unio circulus* Lewis, '71.—*Unio circulus* Pilsbry & Rhoads, '96.—*Obovaria circulus* Ortmann, '12b (anatomy).—*Obovaria (Obovaria) circulus* Simpson, '14, p. 291.—*Obovaria subrotunda* Vanatta, '15, p. 552.

The identity of *Obliquaria subrotunda* and *Obovaria striata* Rafinesque with *U. circulus* Lea has been recognized by Conrad in 1834, who selected *subrotunda* as name, which thus must be used.

Apparently rare in the upper Tennessee region. Reported from the Tennessee below Knoxville (Lewis), and at Knoxville (Call,

and Pilsbry & Rhoads). I know it only from the Holston River at Mascot, Knox Co., where I found three specimens with the diameter of 60, 61 and 62 per cent. of the length. These must be placed with typical *subrotunda* (diameter 60 per cent. and over). A fourth specimen, found associated with these has the diameter of 55 per cent., and should be called *O. subrotunda levigata* (which see).

In this region, there is evidently no tendency of this form to go into the small streams of the headwaters, although my specimens from the Holston indicate an inclination toward the small stream form *levigata*.

Type locality: Ohio River (type from Kentucky River, according to Vanatta).

53. OBOVARIA (OBOVARIA) SUBROTUNDA LEVIGATA
(Rafinesque), 1820.

Unio levigata Rafinesque, '20.—*Obovaria (Obovaria) lens* Simpson, '14, p. 293.—*Obovaria levigata* Vanatta, '15, p. 552.

Already Conrad (1834) has seen that *levigata* Raf. is the same as *lens* Lea.

This is the small stream form of the main species, distinguished by greater compression of the shell (diameter less than 60 per cent. of the length). It is quite abundant in the tributaries of the Tennessee below the Walden Gorge (Sequatchie River, Tenn., Flint River and Hurricane Creek, Madison Co., Ala., Elk River and Bear Creek). It intergrades here with the main species, as it does in the upper Ohio region.

From above the Walden Gorge, I have it from South Chickamauga Creek, Ringgold, Catoosa Co., Ga. From the headwaters region, above Knoxville, I have just two specimens from the Holston, one from Mascot, another from Holston Station, Grainger Co., in which the diameter falls under 60 per cent. (to 55 per cent. in the first, to 57 per cent. in the other). I have never seen a trace of this form in the small streams of this region.

Type locality: Kentucky River.

Genus: NEPHRONAIAS Fischer & Crosse (1893).¹

Ortmann, '12b, p. 324.

54. NEPHRONAIAS LIGAMENTINA GIBBA (Simpson), 1900.

Unio ligamentinus Lewis, '71.—*Unio ligamentinus* Pilsbry & Rhoads, '96.—*Nephronaias ligamentina* (incl. *gibba*) Ortmann, '12b, (anatomy).—*Nephronaias ligamentina gibba* Goodrich, '13, p. 94.—*Lampsilis ligamentina gibba* Simpson, '14, p. 82.

The main species is not represented in the upper Tennessee region, although occasional specimens turn up, which are hard to distinguish from it. The var. *gibba* is extremely abundant in all the larger rivers: Powell, Clinch, Holston, French Broad, Tennessee, but in the upstream direction it disappears before it reaches the headwaters region. In the Powell, it has been observed up to Shawanee, Claiborne Co., Tenn.; in the Clinch, up to St. Paul, Wise Co., Va.; in the North Fork Holston, up to Holston Bridge, Scott Co., Va.; in the South Fork, up to Pactolus, Sullivan Co., Tenn. From the French Broad it also enters the lower part of the Nolichucky, at Chunn's Shoals, Hamblen Co., Tenn.

Type locality: "Ohio River and southward."

55. NEPHRONAIAS PECTOROSA (Conrad), 1834.

Unio pectorosus Conrad, May, '34.—*Unio perdix* Lea, August, '34.—*Unio biangularis* Lea, '40.—*Unio biangulatus* Lea, '43.—*Unio biangulatus* Lewis, '71.—*Unio biangularis* Pilsbry & Rhoads, '96.—*Nephronaias perdix* Ortmann, '12b, p. 326 (anatomy).—*Nephronaias perdix* Ortmann, '13b, p. 311.—*Nephronaias perdix* Goodrich, '13, p. 94.—*Lampsilis biangularis* and *perdix* Simpson, '14, pp. 59 and 88.

The date of publication of *U. perdix* Lea is incorrectly given by Simpson as 1827. There is no question that *biangularis* and *perdix* are the same species, and it is quite astonishing that this identity has not been recognized by Simpson. Recently, Frierson has suggested to me that *vittatis* Rafinesque, 1831, from Greene River, Ky., might

¹ Possibly the generic name should be changed to *Actinonaias*; compare Frierson, *Nautilus*, 31, 1917, p. 48.

be this species. However, I hesitate to accept this, till it has been shown that this species actually exists in Greene River.

N. pectorosa is found in the Tennessee below and at Knoxville (Lewis, Pilsbry & Rhoads), but it seems to be rare there. Farther up, it goes into Clinch, Powell, Holston, French Broad, and lower Nolichucky, and it is also in Little River. It ascends toward the headwaters farther than does *N. ligamentina gibba*, and goes, in the Powell, to Pennington Gap, Lee Co., Va.; in the Clinch to Cleveland, Russell Co., Va.; in North Fork Holston, to Saltville, Smyth Co., Va.; in South Fork Holston, to Barron, Washington Co., Va.; and in the Watauga, to Watauga, Carter Co., Tenn. Just in the region, where *N. ligamentina gibba* begins to disappear (north of the Va.-Tenn. state line), *N. pectorosa* is most abundant and in its best development.

Type locality: Elk River, North Alabama.

Genus: AMYGDALONAIAS Fischer & Crosse (1893).

Ortmann, '12b, p. 327.

56. AMYGDALONAIAS TRUNCATA (Rafinesque), 1820.

Truncilla truncata Rafinesque, '20.—*Unio elegans* Lewis, '71.—*Amygdaloniaias elegans* Ortmann, '12b, p. 328 (anatomy).—*Plagiola (Amygdaloniaias) elegans* Simpson, '14, p. 307.—*Plagiola elegans* Vanatta, '15, p. 553.—*Amygdaloniaias truncata* Utterback, '16, p. 148.

Vanatta does not accept Rafinesque's specific name on account of *Unio truncata* Spengler, 1793. However, these do not conflict (Walker, '16).

Not abundant, and missing in the headwaters. Tennessee below Knoxville (Lewis); Clinch River, Solway, Knox Co.; Edgemoor and Clinton, Anderson Co.; Black Fox Ford, Union Co.; Clinch River Station, Claiborne Co.; Oakman, Grainger Co., Tenn. Holston River, McBee Ford, near Hodges, Jefferson Co., Tenn.

Type locality: Ohio River (type from Falls of the Ohio, according to Vanatta).

Genus: PLAGIOLA Rafinesque (1820).

Ortmann, '12b, p. 329.

57. PLAGIOLA LINEOLATA (Rafinesque), 1820.

Obliquaria lineolata Rafinesque, '20.—*Unio securis* Lewis, '71.—*Unio securis* Pilsbry & Rhoads, '96.—*Plagiola securis* Ortmann, '12b, p. 329 (anatomy).—*Plagiola (Plagiola) securis* Simpson, '14, p. 304.—*Plagiola lineolata* Vanatta, '15, p. 553.—*Plagiola securis* Walker, '16, p. 45.

Of the names of Rafinesque (*depressa*, *lineolata*, and *ellipsaria*) given to this species, *lineolata* has been selected by Conrad in 1834. (Walker, l. c.) This name has been used also by Say, Agassiz, and Call.

Only in the larger rivers. Tennessee at and below Knoxville, also at Rathburn, Hamilton Co., Tenn. (Walker collection). In the Clinch at Patton's Ferry, Roane Co. (Pilsbry & Rhoads), and at Offutt, Anderson Co., Tenn. Rare.

Type locality: Falls of the Ohio.

Genus: PARAPTERA Ortmann (1911).

Ortmann, '12b, p. 330.

If the first species (*leptodon*) should actually belong here, the generic name must be dropped in favor of *Leptodea* Rafinesque, '20 (see Frierson, '14a, p. 6). Utterback ('16, p. 151) uses *Lasmonos* Raf.

58. PARAPTERA LEPTODON (Rafinesque), 1820.

Unio leptodon Rafinesque, '20.—*Unio tenuissimus* Lewis, '71.—*Lampsilis (Proptera) leptodon* Simpson, '14, p. 188.—*Lampsilis leptodon* Vanatta, '15, p. 551.—*Lasmosos leptodon* Utterback, '16, p. 156.

A rare shell. Lewis gives it from the Tennessee below Knoxville. In the Walker collection it is from the Clinch, at Needham Ford, Union Co., Tenn., and I found it in the Clinch at Edgemoor, Anderson Co., Tenn. I found it also in the Holston at Holston Station and Noeton, Grainger Co., Tenn.

Type locality: Lower Ohio River (Vanatta says that the type is from Kentucky River).

59. PARAPTERA FRAGILIS (Rafinesque), 1820.

Unio fragilis Rafinesque, '20.—*Unio gracilis* Lewis, '71.—*Unio gracilis* Pilsbry & Rhoads, '96.—*Paraptera gracilis* Ortmann, '12b, p. 331 (anatomy).—*Lampsilis (Proptera) gracilis* Simpson, '14, p. 181.—*Leptodea (?) fragilis* Frierson, '14a, p. 7.—*Lampsilis fragilis* Vanatta, '15, p. 552.—*Lasmonos fragilis* Utterback, '16, p. 152.

In the larger rivers, not rare. Tennessee River, below Knoxville (Lewis) and Holston River, Boyd Island, near Knoxville (Pilsbry & Rhoads). In the lower Nolichucky at Chunn's Shoals, Hamblen Co.; up the Holston to Holston Station, Grainger Co.; in the Clinch up to Clinch River Station, Claiborne Co.; in the Powell River, up to Combs, Claiborne Co., Tenn.

Type locality: Ohio River (the type is, according to Vanatta, from creeks in Kentucky).

Genus: PROPTERA Rafinesque (1819).

Ortmann, '12b, p. 332.

60. PROPTERA ALATA (Say), 1817.

Unio alatus Say, '17.—*Unio alatus* Lewis, '71.—*Unio alatus* Pilsbry & Rhoads, '96.—*Proptera alata* Ortmann, '12b, p. 333 (anatomy).—*Lampsilis (Proptera) alata* Simpson, '14, p. 162.

Common in the larger rivers: Tennessee in Knox Co.; goes up the Clinch to Clinchport, Scott Co., Va.; up the Powell, to Combs, Claiborne Co., Tenn.; it reaches the North Fork Holston at its mouth, at Rotherwood, Hawkins Co., Tenn. It is also in French Broad River, and in the lower part of the Nolichucky at Chunn's Shoals, Hamblen Co., Tenn.

Type locality: ?

Genus: TOXOLASMA Rafinesque (1831).

Corunculina (error typ.) Simpson, '98.—*Carunculina* Ortmann, '12b, p. 337; '14, p. 68.—*Toxolasma* Frierson, '14a, p. 7.

61. *TOXOLASMA LIVIDUM* (Rafinesque), 1831.

Unio lividus Rafinesque, '31.—*Unio moestus* Lea, '41.—*Unio cylindrellus* Lea, '68.—*Unio glans* Lewis, '71.—*Unio glans* Pilsbry & Rhoads, '96.—*Lampsilis* (*Carunculina*) *cylindrella* and *moesta* Simpson, '14, pp. 155, 156.—*Toxolasma livida* Frierson, '14a, p. 7.

The upper Tennessee form is not the real *U. glans* of Lea ('43), as already hinted at by Pilsbry & Rhoads. The latter is more swollen, and has more inflated beaks, and possibly, it is the big river and lowland form of *Toxolasma lividum*.

What Lea has described as *U. moestus* (from French Broad River, Tenn.) undoubtedly is this: I have specimens from Little Pigeon River (tributary to French Broad), which are fully identical with *moestus*. *U. cylindrellus* Lea (Duck River, Tenn.) is in shape absolutely identical with *T. lividum*; however, it differs by paler color of epidermis and nacre. Such pale specimens occasionally are found in the upper Tennessee drainage as individual variations. Yet it might be, that elsewhere (Tennessee drainage in northern Alabama, and Alabama drainage in Alabama and Georgia) this pale form becomes a distinct race.

U. pullus Conrad, '38, from the original locality, Wateree River, S. Car., may be a different species. But it is rather sure that the specimens from "Warm Springs, N. Car." (= Hot Springs, Madison Co., N. Car., on the French Broad) are actually *T. lividum*.

There is great variation in the color of the nacre: it may be entirely dark purple, or may have (generally) a whitish margin along the edge of the shell; or it may (very rarely) have a pale, yellowish, color. The epidermis is mostly blackish or blackish brown, but it may become pale brown or greenish brown.

This species seems to have a wide range over the upper Tennessee drainage, but, on the other hand, it seems to be rather local. I know it from the following localities: South Fork Powell River, Big Stone Gap, Wise Co., Va. (Walker coll.); Powell River, Jonesville, Lee Co., Va. (Walker coll.); Shawanee, Claiborne Co., Tenn. (Walker coll.); Green's Ford, Union Co., Tenn. (Walker coll.); Clinch River, Speer's Ferry, Scott Co., Va.; Emory River, Harri-

man, Roane Co., Tenn.; North Fork Holston River, at Saltville, Smyth Co. (O. A. Peterson), and at Holston, Washington Co., Va. (Walker coll.); Holston Bridge, Scott Co., Va. (Walker coll.); Holston River, Rogersville (=Austin Mill), Hawkins Co., Tenn. (Walker coll.); Little Pigeon River, Sevierville, Sevier Co., Tenn.; Pistol Creek, Rockford, Blount Co., Tenn. In addition, it is in Lewis's list from the Tennessee below Knoxville.

Type locality: Rockcastle River, Ky. Its actual presence in Rockcastle River, at Livingston, Rockcastle Co., Ky., has recently been confirmed by Williamson (as *U. glans*, see: Ohio Naturalist, 5, 1905, p. 311). Wilson & Clark, '14, do not give it from this place, but I have seen specimens in the Walker coll. from this locality.

Note: This form is also present in the tributaries of the Tennessee in North Alabama, as has been indicated long ago by Conrad. It also seems to be represented in the Alabama drainage, but from this region it generally goes under the name of *corvunculus* Lea, '68. I have a number of specimens of the latter before me, which I cannot distinguish from the upper Tennessee form.

Genus: LEMIOX Rafinesque (1881).

Frierson, '14a, p. 7.—Ortmann, '16, p. 39.

62. LEMIOX RIMOSUS (Rafinesque), 1831.

Unio rimosus Rafinesque, '31.—*Unio calatus* Lewis, '71.—*Micromya calata* Goodrich, '13, p. 94.—*Micromya calata* Simpson, '14, p. 34.—*Lemiox rimosus* Frierson, '14a, p. 7.—*Lemiox rimosus* Ortmann, '16, p. 39 (anatomy):

This species has been reported from the Tennessee below Knoxville (Lewis), and from Powell, Clinch, and Holston rivers (Call). It seems to have a wide distribution, but it is found nowhere in great numbers, and is thus a rare shell. In the Powell, it goes up to Jonesville, Lee Co., Va.; in the Clinch, to St. Paul, Wise Co., Va.; in the North Fork Holston, to Holston, Washington Co., Va. It is found here and there in the Holston proper and the lower Clinch, but I have never seen it in the eastern tributaries of the Holston-Tennessee system.

Type locality: Cumberland River (not reported from the Cumberland drainage by Wilson & Clark, '14).

Genus: MEDIONIDUS Simpson (1900).

Ortmann, '12b, p. 334; '15, p. 143.

63. MEDIONIDUS PLATEOLUS (Rafinesque), 1831.

Unio plateolus Rafinesque, '31.—*Unio conradicus* Lewis, '71.—*Unio conradianus* Pilsbry & Rhoads, '96.—*Medionidus conradicus* Ortmann, '12b, p. 335, and '15, p. 142 (anatomy).—*Medionidus conradicus* Ortmann, '13b, p. 311.—*Medionidus conradicus* Goodrich, '13, p. 94.—*Medionidus conradicus* Simpson, '14, p. 247.

The identity of *U. plateolus* and *conradicus* Lea ('34) has been suggested to me by Frierson, and I think, this is correct.

Very abundant in the headwaters and in small streams generally, but quite rare in the larger rivers. It has been found practically all over our region, and often goes up into the smallest streams which contain at all *Nayades*. It is hardly worth while to record single localities, and it suffices to say that it is in the Powell, Clinch, and Holston, and their tributaries; in the French Broad, it goes up to Asheville, N. Car.; it is in Little River, and in South Chickamauga Creek, Ga. From the Tennessee proper, below Knoxville, it has been reported by Lewis.

Type locality: Falls of the Cumberland River. (Its existence at this place, below the falls, has been confirmed by Wilson & Clark, '14.)

Genus: EURYNIA Rafinesque (1820).

Ortmann, '12b, p. 336.

64. EURYNIA (MICROMYA) FABALIS (Lea), 1831.

Unio fabalis Lea, '31.—*Unio fabalis* Lewis, '71.—*Eurynia (Micromya) fabalis* Ortmann, '12b, p. 339 (anatomy).—*Eurynia fabalis* Goodrich, '13, p. 94.—*Micromya fabalis* Simpson, '14, p. 33.

Rather rare, but possibly in part overlooked. Lewis gives it from Tennessee River, below Knoxville, and the Walker collection

has it from Tennessee River, Little River Shoals, Knox Co., Tenn. I found it chiefly toward the headwaters, in Powell, Clinch, and Holston. In the Powell, it goes up to Combs, Claiborne Co., Tenn.; in the Clinch, to Cleveland, Russell Co., Va.; in the North Fork Holston, to Hilton, Scott Co., Va.; in the South Fork, to Pactolus, Sullivan Co., Tenn. It seems to be absent from the eastern tributaries of the system.

Type locality: Ohio River.

65. EURYNIA (MICROMYA) TRABALIS (Conrad), 1834.

Unio trabalis Conrad, '34.—*Eurynia (Micromya) trabalis* Ortmann,

Extremely rare. I found a single specimen in Clinch River, at Speer's Ferry, Scott Co., Va.; another one in South Chickamauga Creek, Ringgold, Catoosa Co., Ga.; and three specimens in Hiwassee River, at Austral, Polk Co., Tenn. At the first locality, it was associated with the next species.

The only difference of *E. trabalis* and *perpurpurea* is, that the former has white, the latter purple nacre. The specimens from the Hiwassee are exceptionally large, and do not taper so much behind as usual.

This species seems to have its metropolis in the Cumberland system (Wilson & Clark, '14). Call cites it from Clinch and Powell Rivers in Tennessee, but Lewis does not mention it from the "Holston" (=Tennessee), and I have never seen a trace of it in the whole Holston drainage. According to Hinkley, it is rare in the mussel shoals of the Tennessee in Alabama; the Carnegie Museum has one specimen from Paint Rock River, at Paint Rock, Jackson Co., Ala. It may be that my localities in Chickamauga Creek and Hiwassee River are connected with the range in northern Alabama.

Type locality: ?

66. EURYNIA (MICROMYA) PERPURPUREA (Lea), 1861.

Unio perpurpurea Lea, '61.—*Eurynia perpurpurea* Ortmann, '13b, p. 311.—*Eurynia purpurpurea* Goodrich, '13, p. 94.—*Lampsilis perpurpurea* Simpson, '14, p. 133.—*Eurynia (Micromya) perpurpurea* Ortmann, '15, p. 63 (anatomy).

'12b, p. 340 (anatomy).—*Lampsilis trabalis* Simpson, '14, p. 132.

This may be only a variety with purple nacre of *E. trabalis*, but I have not yet seen any intergrades.

It is characteristic for the Clinch River, where it is not rare in Virginia (from Speer's Ferry, Scott Co., up to Cedar Bluff, Tazewell Co.). In addition, it is in the Powell at Olinger, Lee Co., Va. (Walker coll.); in the North Fork Holston, from Rotherwood, Hawkins Co., Tenn., to Mendota, Washington Co., Va.; and in Emory River, Harriman, Roane Co., Tenn.

In the Tennessee and Holston proper, and their eastern mountain tributaries, no trace of this species has ever been found.

Type locality: Tennessee.

67. EURYNIA NEBULOSA (Conrad), 1834.

Unio nebulosus Conrad, '34.—*Unio cumberlandianus* Lea, '36.—*Unio cumberlandicus* Lea, '38.—*Unio notatus* Lea, '38.—*Unio glaber* Lea, '38.—*Unio creperus* Lea, '38.—*Unio muehlfeldianus* Lea, '38.—*Unio simus* Lea, '38.—*Unio obscurus* Lea, '38.—*Unio zeiglerianus* Lea, '38.—*Unio amœnus* Lea, '40.—*Unio fatuus* Lea, '40.—*Unio dactylus* Lea, '40.—*Unio tener* Lea, '40.—*Unio regularis* Lea, '41.—*Unio puniceus* Haldeman, '42.—*Unio radians* Lea, '57.—*Unio jonesi* Lea, '59.—*Unio discrepans* Lea, '60.—*Unio scitulus* Lea, '60.—*Unio linguæformis* Lea, '60.—*Unio perpictus* Lea, '60.—*Unio planicostatus* Lea, '60.—*Unio sparus* Lea, '68.—*Unio dispansus* Lea, '71.—*Unio glaber, iris, cumberlandianus, jonesi, sparus* Lewis, '71, and '72.—*Unio muhlfeldtianus* Pilsbry & Rhoads, '96.—*Eurynia nebulosa, dispansa, and planicostata* Ortmann, '13b, p. 311.—*Eurynia nebulosa* Goodrich, '13, p. '94.—*Eurynia (Micromya) nebulosa* Ortmann, '15, p. 64 (anatomy).

Simpson, '14, has recognized the identity of a great number of these nominal "species," but not of all of them. He gives (pp. 119 and 120): *cumberlandianus* (Cumberland R., Tenn.); *notatus* (Cumberland and Holston R., Tenn.); *glaber* (Holston R., Tenn.); *radians* (Othcalooga Cr., Gordon Co., Ga.); *jonesi* (Euharlee Cr., Ga.); *discrepans* (North Alabama); *scitulus* (Tuscumbia, Ala.); *linguæformis* (Columbia, Ga., and French Broad R., Tenn.); *perpictus* (Bull R.

and Holston R.) ; *sparus* (Swamp Cr., Whitfield Co., Ga.), and I am fully convinced that all these actually are synonyms of *nebulosus*. But I believe that there are many others, and on account of the extraordinary size of the list of synonyms, I think it advisable to make a few remarks as to these.

U. creperus Lea, '38 (Tennessee), made a synonym of *L. iris* (Lea) by Simpson (p. 115), is founded upon an old half shell, hardly recognizable, but it may be this. In the Walker collection is a specimen from Clinch R., Va. (Wright), labeled *creperus*, which is distinctly *E. nebulosa*. It is a male, has purple nacre, and distinct, rather broad, only slightly interrupted rays.

U. dispansus Lea, '71 (east Tennessee), has been put by Simpson (p. 106) in the synonymy of *L. vanuxemensis*; I think it belongs here.

U. puniceus Haldeman, '42 (Simpson, p. 104) (Holston R., Washington Co., Va.). I have found forms corresponding to the description in the same region (topotypes), and they simply are *E. nebulosa* with a peculiar reddish-orange nacre.

U. obscura Lea, '38 (Nashville, Tenn.), and *U. zeiglerianus* Lea, '38 (Cumberland R., Tenn.), made synonyms by Simpson (p. 117) are also this, with rather fine, uninterrupted rays, and purple nacre.

U. fatuus Lea, '40 (Holston R., Tenn.), and *U. dactylus* Lea, '40 (Caney Fork R., Tenn.), made synonyms by Simpson (pp. 116, 117), are rather elongated and unusually swollen forms of *E. nebulosa*, with the rays less developed, and not interrupted.

U. planicostatus Lea, '60 (Tuscumbia, Ala.) (Simpson, p. 117). A strongly compressed male, with rays distinct, rather wide, and little interrupted. Such specimens are frequent, chiefly in the Clinch.

U. muehlfeldianus Lea, '38 (Cumberland R., Tenn.) (Simpson, p. 121). According to Simpson, only a single specimen is known, which is undoubtedly this, probably a female. Pilsbry & Rhoads give this also from Watauga R., near Johnson City, Washington Co., Tenn.: near this place (Watauga, Carter Co.), I have found *E. nebulosa*.

U. amarus Lea, '40 (Holston R., Tenn.) (Simpson, p. 122). A typical female of *E. nebulosa*.

U. tener Lea, '40 (Big Pigeon R., Tenn.) and *U. regularis* Lea,

'41 (French Broad R., Tenn.), made synonyms by Simpson (pp. 122, 123). There are two specimens (♂ and ♀) in the Walker collection, labeled *tener* (from French Broad, Asheville, N. Car.). They are rather thin-shelled, have rays, which are fine, and subcontinuous in the male, but somewhat spotted in the female. They undoubtedly are a form of *E. nebulosa*.

U. simus Lea, '38 (Cumberland R., Tenn.) (Simpson, p. 123). A male, with strongly developed rays: specimens of this type occur frequently, and are practically identical with *U. notatus*, admitted by Simpson as a synonym of *nebulosus*.

This tremendous synonym indicates that we have to deal here with a very variable species. The variation concerns first of all the color pattern of the epidermis (rays). In the second line it is shown in the color of the nacre, the shape of the shell, and, of course, sometimes the females have been made "species" for the reason of their different shape. It is not excluded that additional synonyms may be discovered.

E. nebulosa belongs in the affinity of *E. iris* (Lea), '30, and has practically the same anatomy. Indeed, some of its forms are hardly distinguishable from *E. iris*, and it may be that the latter is only the western and northwestern representative of it (that of the Ohio drainage). Thus it is also explained why *iris* has been recorded for the upper Tennessee River (Lewis).

According to my observations, there is only *one* species of the *iris*-group in the upper Tennessee region. It is generally an elongated-elliptical shell, more or less pointed behind in the male, slightly dilated and rounded posteriorly in the female, of a yellowish, greenish, or brownish color, covered more or less with rays, which normally are well developed, and very often broken up into spots. These rays may be fine or wide (in the female, they are often very broad and distinct on the dilated part of the shell), may cover all of the shell, or only part of it, and may be indistinct or nearly missing. The interior of the shell may be white, or of all shades of salmon, orange, pink, or purple.

Although I have tried hard, I have been unable to separate this group of forms into species, and it is also impossible for me to distinguish local races. It is true that sometimes specimens from a cer-

tain locality, chiefly from some small creeks, show uniform and peculiar characters, but this holds good only for short distances. In the longer rivers (Powell, Clinch, Holston) the variation is considerable and irregular, apparently without any recognizable rules.

The distribution of *E. nebulosa* extends over the whole of the upper Tennessee region, but the species decidedly favors the headwaters and small streams, and often goes up to the uppermost limit of Nayad-distribution in this region. It is not necessary to give a list of the localities: it is practically everywhere in the Powell, Clinch, Holston, French Broad, Little River, Hiwassee. (It apparently is only accidental that it has not been recorded from the Little Tennessee.) It is also in Chickamauga Creek, and it deserves special mention that it goes up, in French Broad, to Asheville, N. Car.

In the larger rivers, this species is rare, yet it is present.

In addition, *E. nebulosa* has a wide range not only in the Cumberland drainage, but also in that of the Tennessee in North Alabama, and it also has invaded the headwaters of the Coosa-Alabama system in northern Georgia and Alabama. It is very singular that Wilson & Clark ('14) do not mention it in their paper on the Cumberland shells, although a good number of the synonyms have their type locality in this system.

Type locality: Black Warrior River, Ala.

68. EURYNIA (MICROMYA) VANUXEMENSIS (Lea), 1838.

Unio vanuxemensis Lea, '38.—*Unio nitens* Lea, '40.—*Unio umbrus* Lea, '57 (= *umbrans* Lea, '57).—*Unio tenebricus* Lea, '57.—*Unio pybasi* Lea, '58.—*Unio fabaceus* Lea, '61.—*Unio copei* Lea, '68.—*Unio pybasi* Lewis, '71.—*Unio pybasi* and *caliginosus* Pilsbry & Rhoads, '96.—*Eurynia (Micromya) vanuxemensis* Ortmann, '12b, p. 342.—'15, p. 65 (anatomy).—*Nephronaias copei* and *Eurynia vanuxemensis* Ortmann, '13b, p. 311.—*Eurynia vanuxemensis* Goodrich, '13, p. 95.—*Lampsilis vanuxemensis* Simpson, '14, p. 105.

Unio dispansus Lea, '71, placed by Simpson here, belongs to *E. nebulosa* (see above). Probably there are other synonyms.

This shell is shorter and higher than *E. nebulosa*, has generally a

dark epidermis with indistinct or no rays, and a deep copper-colored or purplish nacre; rarely the latter is lighter, and even when whitish, it has at least some purple or red. The female is characterized by a very strong dilatation of the postbasal margin, and very often, chiefly in old shells, it has a strong "constriction" behind this dilatation.

The distribution of this species is very similar to that of *E. nebulosa*, preferring also the small streams, and very often the two species are found associated. Also here it is unnecessary to give a list of localities, and it suffices to state that it is found practically over the whole upper Tennessee region. It should be remarked, however, that I did not find it in the headwaters of the Clinch (above Speer's Ferry, Va.), but it may have been overlooked here. While locally abundant in smaller streams, it becomes rare in the larger rivers.

Also here, local races cannot be distinguished, except that the shell attains, in certain streams, a much greater size than in others. This is the case, for instance, in the Middle Fork Holston in Smyth Co., Va., where exceptionally large specimens (*U. copei* Lea) are found, while the North Fork contains a small race. Specimens of larger rivers are also generally rather large and well developed, and often lack, in the ♀, the posterior constriction. Such specimens have a resemblance to *U. lienosus* Conrad, being more drawn out at the posterior end. *U. lienosus* is a southern form, not found in the Tennessee drainage. There is no doubt that *U. caliginosus* Lea (= *lienosus*), recorded by Pilsbry & Rhoads from the lower Clinch, is founded upon such specimens.

Also this species has a wide distribution in the Cumberland drainage, the Tennessee drainage in Alabama, and the Coosa-Alabama system, and it is very likely that also the form of the Cumberland, questionably referred to *lienosa* by Wilson & Clark ('14), is this.

Type locality: Cumberland River, Tenn.

69. EURYNIA (EURYNIA) RECTA (Lamarck), 1819.

Unio rectus Lamarck, '19.—*Unio rectus* Lewis, '71.—*Unio rectus* Pilsbry & Rhoads, '96.—*Eurynia (Eurynia) recta* Ortmann, '12b, p. 344 (anatomy).—*Eurynia recta* Goodrich, '13, p. 95.—*Lamp-silis recta* Simpson, '14, p. 95.

Abundant in the larger rivers: Tennessee in Knox Co., lower

French Broad and lower Nolichucky (Hamblen Co.); all the way up the Holston to the North Fork at Rotherwood, Hawkins Co., Tenn. Also in the Clinch up to St. Paul, Wise Co., Va., and the Powell up to Combs, Claiborne Co., Tenn.

Type locality: Lake Erie (topotypes examined).

Note: The Lake Erie form differs somewhat from that of the central basin. If it should be found to be desirable to express this in nomenclature, *E. recta* should be reserved for the lake form, and *E. recta latissima* (Rafinesque), '20, should be used for the other.

Genus: LAMPSILIS Rafinesque (1820).

Ortmann, '12b, p. 345.

70. LAMPSILIS VIRESCENS (Lea), 1858.

Unio virescens Lea, '58.—*Lampsilis virescens* Simpson, '14, p. 93.

I am not quite satisfied as to the proper position of this species within the genus *Lampsilis*. According to external appearance, it seems to be related to *L. luteola* (Lam.), although it also has some features, which resemble those of *L. teres* (Raf.) (= *anodontoides* Lea). In either case, however, it would be a *Lampsilis*.

The *type locality* is Tennessee River, Tusculumbia, Colbert Co., Ala., and it has been reported, by Call, from Spring Creek at Tusculumbia. The Carnegie Museum has it from tributaries of the Tennessee in northern Alabama (Paint Rock River, and Bear Creek). It has never been found anywhere else.

But I have found a few specimens (all males) in Emory River, at Harriman, Roane Co., Tenn., and in the Walker collection are others from Coal Creek, Anderson Co., Tenn. These two streams are not far apart, and flow from Walden Ridge to the Clinch. Emory River is the only western tributary which completely cuts through Walden Ridge and drains, in its headwaters, a section of the Cumberland Plateau.

71. LAMPSILIS OVATA (Say), 1817.

Unio ovatus Say, '17.—*Unio ovatus* Lewis, '71.—*Unio ovatus* Pillsbry & Rhoads, '96.—*Lampsilis ovata* Ortmann, '12b, p. 350 (anatomy).—*Lampsilis ovata* Simpson, '14, p. 48.

Distinguished by the distinct and sharp posterior ridge, depressed (truncated) posterior slope, and the peculiar, wedge-shaped anterior part of the shell. But these characters gradually pass into those of the variety *ventricosa*.

The typical *L. ovata* is restricted to the larger rivers, and quite abundant there. It is in the Tennessee, the Little Tennessee, Holston, Clinch, and Powell. In the Powell, it goes up to Shawanee, Claiborne Co., Tenn.; in the Clinch, to Clinchport, Scott Co., Va. It is the prevailing form in the Holston proper, but does not go into the Forks of the Holston. All along its range, and chiefly *above* Knoxville, it is accompanied by the var. *ventricosa*, and intergrades with it. But at the points just named, it disappears, and leaves the field to *ventricosa*.

Type locality: Ohio River.

72. LAMPSILIS OVATA VENTRICOSA (Barnes), 1823.

Unio ventricosa Barnes, '23.—*Lampsilis ventricosa* Ortmann, '12b, p. 351 (anatomy).—*Lampsilis ovata ventricosa* Ortmann, '13b, p. 311.—*Lampsilis ovata ventricosa* Goodrich, '13, p. 95.—*Lampsilis ventricosa* Simpson, '14, p. 38.

According to Vanatta ('15, p. 551), the type of *Lampsilis cardium* Rafinesque, '20, is this, and also Conrad ('34) says so. However, this conflicts with Rafinesque's description, from which it is evident that *L. cardium* is the female of *L. ovata*. We have here a case where the "type" does not agree with the original description, and it should be borne in mind that the co-called "types" of Rafinesque, in the Philadelphia Academy, are not types in the strict sense, but merely "authentic specimens" of somewhat doubtful value.

In this variety, the posterior ridge becomes indistinct, the posterior slope is not excavated, and the anterior part of the shell is not remarkably compressed. Also, the shell is generally less convex. But there are all stages of transition. The upper Tennessee form of *ventricosa* very rarely has the distinct rays of the corresponding form of the upper Ohio region.

L. ovata ventricosa is found associated with the normal *L. ovata* in the larger rivers, but is less frequent there. It goes, however,

beyond the upper limit of *L. ovata* in the headwaters, where it is found in its best development and as a pure race. In the Powell, it goes to Olinger, Lee Co., Va.; in the Clinch, to Cedar Bluff, Tazewell Co., Va.; in North Fork Holston, to Saltville, Smyth Co., Va. (also in Big Mocassin Creek); and in the South Fork, to Emmett, Sullivan Co., Tenn. It is in Nolichucky River, at Chunn's Shoals, Hamblen Co., Tenn. (inclining here toward *ovata*); in Little Pigeon River, Sevierville, Sevier Co., Tenn.; in Little River, Melrose, Blount Co., Tenn.; and in Emory River, Harriman, Roane Co., Tenn. I have seen it also in Chickamauga Creek, Ringgold, Catoosa Co., Ga.

Type locality: Wisconsin River, and Mississippi River, Prairie du Chien, Wis.

73. *LAMPSILIS FASCIOLA* Rafinesque (1820).

Lampsilis fasciola Rafinesque, '20.—*Unio multiradiatus* and *perradiatus* Lewis, '71.—*Unio multiradiatus* Pilsbry & Rhoads, '96.—*Lampsilis multiradiata* Ortmann, '12b, p. 352 (anatomy).—*Lampsilis multiradiata* Ortmann, '13b, p. 311.—*Lampsilis multiradiata* Goodrich, '13, p. 95.—*Lampsilis multiradiata* Simpson, '14, p. 55.

Also in this case, I do not follow Vanatta's ('15, p. 551) determination of the "type" of *fasciola*, but rely on Rafinesque's description, which indicates a shell of the *cardium-ovata* type, with unequal, flexuous rays, which fits *multiradiata* Lea, but not *luteola* Lamarck. Moreover, Conrad, in 1836, held the same opinion, also pointing out the undulated rays as the main character of this species.

Practically everywhere in the larger rivers as well as in smaller streams, but apparently more abundant toward the headwaters. In the Tennessee, South Chickamauga, Hiwassee, Little Tennessee, Little River. In the French Broad drainage, going up here to Asheville, N. Car., and, in Big Pigeon River, to Canton, N. Car. In the Holston, up to the South Fork at Barron, Washington Co., Middle Fork at Chilhowie, Smyth Co., and North Fork at Saltville, Smyth Co., Va. Also in Big Mocassin Creek, and Watauga River. In the Clinch, it goes up to Cedar Bluff, Tazewell Co., Va.; in the Powell, to the North Fork at Big Stone Gap, Wise Co., Va. Also in the Emory at Harriman, Roane Co., Tenn.

Type locality: Kentucky River.

74. *LAMPSILIS ORBICULATA* (Hildreth), 1828.

Unio orbiculatus Hildreth, '28.—*Lampsilis orbiculata* Ortmann, '12b, p. 343 (anatomy).—*Lampsilis orbiculata* Simpson, '14, p. 76.

Not reported previously from the upper Tennessee region, but in the Walker collection are two specimens labeled "Holston R., Tenn.," which come from the Lewis collection (and thus probably are from the Tennessee). I have found myself two specimens in the Clinch, one at Offutt, Anderson Co., the other at Solway, Knox Co., Tenn.

This species is also in the Tennessee in North Alabama, at the mussel shoals near Florence (reported by Hinkley, and represented in Walker coll. and Carnegie Mus.).

Type locality: Muskingum River, Marietta, Ohio.

Genus: *TRUNCILLA* Rafinesque (1820).

Ortmann, '12b, p. 354.

The subgenera distinguished by Simpson require revision, also with regard to nomenclature. I disregard them for the present, remarking only that the soft parts furnish good criteria for their definition.

75. *TRUNCILLA TRIQUETRA* Rafinesque, 1820.

Truncilla triqueter Rafinesque, '20.—*Unio triangularis* Lewis, '71.—*Unio triangularis* Pilsbry & Rhoads, '96.—*Truncilla triquetra* Ortmann, '12b, p. 355 (anatomy).—*Truncilla triquetra* Simpson, '14, p. 5.

Rather frequent both in larger and smaller rivers, but nowhere in great numbers. Tennessee below Knoxville (Lewis) and at Knoxville (Pilsbry & Rhoads); Little River in Knox Co. (Walker coll.); lower Nolichucky; Holston River up to the South Fork at Pactolus, Sullivan Co., Tenn., and the North Fork at Mendota, Washington Co., Va.; in the Clinch up to Clinchport, Scott Co., Va.; in the Powell, up to Shawanee, Claiborne Co., Tenn.

Type locality: Falls of the Ohio.

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76. TRUNCILLA ARCÆFORMIS (Lea), 1831.

Unio arcæformis Lea, '31.—*Unio arcæformis* Lewis, '71.—*Unio arcæformis* Pilsbry & Rhoads, '96.—*Truncilla arcæformis* Simpson, '14, p. 12.

In the larger and medium rivers: Tennessee, Knox Co., Tenn.; French Broad at Boyd Creek, Sevier Co. In the Holston locally abundant: Boyd Island, near Knoxville (Pilsbry & Rhoads); McMillan, Knox Co.; Mascot, Knox Co.; Gant Island near Strawberry Plains, Jefferson Co. (Walker coll.); McBee Ford, near Hodges, Jefferson Co.; Turley Mill, Noeton, and Holston Station, Grainger Co.; Austin Mill, Hawkins Co., Tenn. In the Clinch at Clinch River Station, Claiborne Co.; and Oakham, Grainger Co., Tenn.

Type locality: "Tennessee River." Lea (Tr. Amer. Philos. Soc., 1834, p. 86) corrects this, saying that, according to Troost, this species is not in the Tennessee, but only in the Cumberland River (meaning, of course, the Tennessee of northern Alabama).

77. TRUNCILLA INTERRUPTA (Rafinesque), 1820.

Obliquaria interrupta Rafinesque, '20.—*Unio brevidens* Lea, '31 (not '34, as given by Simpson).—*Unio brevidens* Lewis, '71.—*Truncilla brevidens* Simpson, '14, p. 7.

The identity of Rafinesque's species with that of Lea has been recognized by Conrad, accepted by Kuester and Reeve, and confirmed by Vanatta ('15, p. 550). But Vanatta does not use the name of *interrupta*, for reasons which do not hold good, as shown by Walker ('16, p. 45). The only objection to *interrupta* is that it is given, originally, from Kentucky and Ohio rivers, while it seems to be absent at least from the Ohio. But we must remember that Lea's *brevidens* also was originally given from Ohio, corrected subsequently, '34, to Cumberland River.

In the larger and medium rivers: Tennessee (Lewis), Holston, Clinch, and Powell. In the Powell, up to Rose Hill, Lee Co., Va.; in the Clinch, up to Clinchport, Scott Co., Va.; in the Holston up to the North Fork at Hilton, Scott Co., Va.

Type locality: "Kentucky and Ohio Rivers." (Probably incorrect; type from Ohio River, according to Vanatta.)

78. *TRUNCILLA LENIOR* (Lea), 1843.

Unio lenior Lea, '43.—*Truncilla lenior* Simpson, '14, p. 11.

A rare species. I have found it in the Clinch, Speer's Ferry, Scott Co., Va.; in North Fork Holston, Rotherwood, Hawkins Co., Tenn.; in South Fork Holston, Pactolus, Sullivan Co., Tenn.; and in the uppermost Holston proper, Church Hill, Hawkins Co., Tenn.

There are specimens in the Walker coll. (from Mrs. Andrews), labeled: Holston River, Knox Co. (probably Tennessee River), but Lewis has not recorded it from these parts. For the rest, it is missing in this region, but it turns up again in the Tennessee drainage in North Alabama: Simpson gives it from Paint Rock River, Woodville, Jackson Co., Ala., and the Carnegie Museum possesses quite a number of specimens from this river at Paint Rock, Holly Tree, and Trenton, Jackson Co., Ala.

The male of this species may be easily recognized by the fine denticles on the margin of the posterior end; for the rest, it looks like a pale-colored *Eurynia nebulosa*.

Type locality: Stones River, Tenn. (Cumberland drainage; but missing in the list of Cumberland shells published by Wilson & Clark, '14).

79. *TRUNCILLA HAYSIANA* (Lea), 1833.

Unio haysianus Lea, '33.—*Unio haysianus* Lewis, '71.—*Unio haysianus* Pilsbry & Rhoads, '96.—*Truncilla haysiana* Ortmann, '12b, p. 357 (anatomy).—*Truncilla haysiana* Ortmann, '13b, p. 311.—*Truncilla haysiana* Goodrich, '13, p. 95.—*Truncilla haysiana* Simpson, '14, p. 16.

Widely distributed, but always only in small numbers at a given locality. Tennessee in Knox Co. (Lewis) and at Knoxville (Pilsbry & Rhoads); Little Tennessee, Coytee, Loudon Co., Tenn. (Walker coll.); in the Powell, up to Pennington Gap, Lee Co., Va.; in the Clinch, up to Raven, Tazewell Co., Va.; in the Holston, it goes in the North Fork to Hilton, Scott Co., Va., and in the South Fork to Pactolus, Sullivan Co., Tenn.

Type locality: Cumberland River.

80. *TRUNCILLA STEWARDSONI* (Lea), 1852.

Unio stewardsoni Lea, '52.—*Unio stewardsoni* Lewis, '71.—*Truncilla stewardsoni* Simpson, '14, p. 21.

I think that what Walker ('10a, pl. 3, f. 4) has figured as the ♂ of *T. lewisi* is actually an old ♂ of *stewardsoni*.

A rare species. The Carnegie Museum has specimens from the Tennessee at Knoxville, and Lewis reports it from this region; and there are also specimens from Clinch River, Clinton, Anderson Co., in the Carn. Mus. I found it myself in the Holston, at McMillan and Mascot, Knox Co., and at Holston Station, Grainger Co., Tenn.

Type locality: "Chattanooga River, Tenn." There is no such river in Tennessee. Generally, Lea's "Chattanooga River" is the Chattooga River in northern Georgia (tributary to Coosa); but in the present instance this cannot be, since this species is not found in the Coosa drainage.

81. *TRUNCILLA LEWISI* Walker (1910).

Unio foliatus Lewis, '71.—*Truncilla lewisi* Simpson, '14, p. 20.

As stated above, Walker's figure of the ♂ ('10a, pl. 3, f. 4) probably belongs to *T. stewardsoni*.

I have found a single small male specimen (soft parts examined!) in the Holston, at Holston Station, Grainger Co., Tenn., and another, somewhat larger one, in the Powell, at Combs, Claiborne Co., Tenn. These differ from the male of *T. stewardsoni* by a wider radial furrow, with the two ridges confining it, more divergent. My specimens are not full grown, and even if they should be young females (as Walker suggested after examination of the one from the Holston), they would present to us the shape of the male, as all young females do in the genus *Truncilla*, exactly as the soft parts of young females resemble those of the males.

The Carnegie Museum has (from the Hartman coll.) two females, labeled: Tennessee River, Knox Co., Tenn. Lewis gives this form (as *U. foliatus*) from the Tennessee at Little River Shoals, below Knoxville; and Walker reports it from Clinch and Holston rivers in Knox Co. (also from Cumberland River, Burnside, Pulaski Co., Ky., but not found here by Wilson & Clark, '14).

Thus this is undoubtedly one of the rarest species of *Truncilla*, and its distribution should be studied more closely.

Type locality: Holston River, Tenn. (topotype examined).

82. *TRUNCILLA PROPINQUA* (Lea), 1857.

Unio propinquus Lea, '57.—*Unio propinquus* Lewis, '71.—*Unio propinquus* Pilsbry & Rhoads, '96.—*Truncilla propinqua* Simpson, '14, p. 27.

Reported, by Lewis, from Tennessee River, Knox Co., and from the Clinch by Call. Pilsbry & Rhoads give it from the Tennessee at Knoxville, the Holston at Boyd Island, near Knoxville, and from the Clinch at Patton's Ferry, Roane Co. The Carnegie Museum possesses it from the Tennessee, Knox Co. (Smith coll.), and I found it myself in the Clinch at Edgemoor and Clinton, Anderson Co., Tenn.

Type locality: Florence and Tuscumbia, Ala. (topotypes examined).

83. *TRUNCILLA TORULOSA* (Rafinesque), 1820.

Amblema torulosa and *gibbosa* Rafinesque, '20.—*Unio perplexus* Lewis, '71.—*Truncilla perplexa* Simpson, '14, p. 24.—*Truncilla torulosa* Vanatta, '15, p. 550.

The identity of *torulosa* and *gibbosa* with *perplexus* has been indicated by Conrad ('34), and he selected the name of *torulosa*. Although he later ('36) uses *gibbosus* (and so do Agassiz and Reeve), the first selection has to stand.

The typical *T. torulosa* has a radial row of prominent knobs across the middle of the shell. But these knobs vary greatly, and in the upstream direction, they have the tendency to become reduced, finally disappearing, thus passing into the condition seen in the next form.

Restricted to the larger rivers. It turns up in the Tennessee at and below Knoxville (Lewis), and continues down the river, but is hardly found above Knoxville. The Carnegie Museum has three young specimens from near Knoxville (Hartman coll.), which have distinct knobs. In addition, there is a specimen from Chattanooga, Hamilton Co., Tenn. (Juny coll.), which is typical in all respects,

except that it has salmon-colored nacre; to my knowledge, this color of the nacre is extremely rare.

Farther down the Tennessee, at the mussel shoals in Alabama, this species is abundant (Conrad, Hinkley, and Carn. Mus.).

Type locality: Ohio River and Kentucky River (the type is from Kentucky River, according to Vanatta).

84. *TRUNCILLA TORULOSA GUBERNACULUM* (Reeve), 1865.

Unio gubernaculum Reeve, Conch. icon. 16. *Unio*. '65, pl. 28, f. 146.

Reeve's figure undoubtedly is this form. Simpson ('14, p. 26) makes this a synonym of the var. *rangiana* (Lea), and it surely is the parallel form to *rangiana* of the upper Ohio drainage. It differs, however, distinctly by the dark green color of the posterior expansion of the female shell.

From the typical *torulosa*, this variety differs by the poorly developed or wanting knobs, and by the rather more compressed shell.

This is the headwaters form of *torulosa*, and begins to take its place in the region of Knoxville. I have it from the Nolichucky, Chunn's Shoals, Hamblen Co.; here, as also in the lower Holston, faint knobs may yet be present. Farther up, the shell is entirely smooth. In the Holston, it goes up to the South Fork at Pactolus, Sullivan Co., Tenn., and to the North Fork at Holston Bridge, Scott Co., Va. In the Clinch, it goes to Dungannon, Scott Co., Va. It is also in the Powell, up to Shawanee, Claiborne Co., Tenn. Locally, it may be quite abundant.

Type locality: ?

85. *TRUNCILLA TURGIDULA* (Lea), 1858.

Unio turgidulus Lea, '58 (male).—*Unio deviatulus* Reeve, '64 (female).—*Truncilla deviata* Walker, '10b, pp. 77, 78, 81.—*Truncilla deviata* Simpson, '14, p. 31.

Unio turgidulus has been regarded as the male of the female *U. florentinus*, but it belongs to the female *deviatulus*. In Walker's key (10b), this has been indicated by the grouping, but it has not been expressly mentioned.

T. turgidula stands nearest to *T. biemarginata* (Lea), a species

known from the Tennessee in North Alabama, but which has not yet been recorded from the upper Tennessee. *T. turgidula* agrees with the latter in the biangulate posterior ridge, but the biangulation is much less pronounced, and the depression or furrow in front of it is less developed. In the female (*deviatus*), the biangulation is also present, but indistinct, and the furrow is obliterated, being filled by the expansion of the shell. The female resembles, to a degree, that of *T. florentina*, but has the shell, as Simpson states, more elongated, and has fuller and higher beaks (the latter characters hold also good for the male).

This species has been recorded from Cumberland and Tennessee rivers (not recently found by Wilson & Clark, '14, in Cumberland), and from Duck River, Tenn. (Call), but only one definite locality is known (Florence, Lauderdale Co., Ala.). Hinkley reports it from Shoals Creek, Lauderdale Co., Ala. The Carnegie Museum has it from Bear Creek, in Franklin Co., Ala. I have found it in the upper Tennessee drainage, where it is not rare in the Holston proper from Knox Co. up to Austin Mill, Hawkins Co., Tenn. I found it also in Emory River, Harriman, Roane Co., Tenn. In the Walker coll. it is represented from the Holston, Rogersville, which is practically the same locality as Austin Mill.

Type locality: Cumberland River and Florence, Ala.

86. *TRUNCILLA FLORENTINA* (Lea), 1857.

Unio florentinus Lea, '57.—*Truncilla florentina* Simpson, '14, p. 30 (excl. *turgidulus*).

This species has not a biangulate posterior ridge, but this ridge is rounded, and the radial depression in front of it is hardly developed, indicated only by a flattening of the shell. In the female, the posterior expansion of the shell may become very large, and is generally of the color of the rest of the shell, or lighter, but not uniformly dark green, as in *T. capsæformis*. By the latter character, by the more strongly developed and more numerous denticulations of the margin of the expansion, and by the greater convexity of the shell, *T. florentina* is distinguished from *capsæformis*. The male of *T. florentina* is shorter, higher, and more swollen than that of *T. capsæformis*.

Known from the Cumberland and Tennessee Rivers, from the latter, however, reported hitherto only from North Alabama. I have found it in the Holston, from Knox Co., up to Holston Station, Grainger Co., Tenn., but not in great numbers.

Type locality: Florence, Ala. (and Cumberland River) (topotypes examined).

87. *TRUNCILLA WALKERI* Wilson & Clark (1914).

Truncilla walkeri Wilson & Clark, '14, p. 46, pl. 1, f. 1.

This is practically a large, compressed *T. florentina*. It agrees with it in every respect, except that it attains a larger size, and is as compressed as *T. capsæformis*. It may be only the headwaters form of *T. florentina*.

From *T. capsæformis* it is distinguished by larger size, and by the absence of any dark green tints (except rays) upon the posterior expansion of the female. Also the denticulations on the margin of the expansion are stronger and more numerous. Wilson & Clark do not mention these denticulations: but his specimens seem to have been more or less mutilated in this region. My specimens, belonging to the type set, show only traces of them, while the fine material I collected myself in the headwaters of the Holston shows them well developed.

The males of *T. walkeri* and *capsæformis* are very similar: that of *walkeri* is possibly somewhat larger and of a lighter color, yellowish brown, with light green rays, while that of *capsæformis* is greenish olive, with dark green rays. But these differences are rather uncertain. However, I was never put to the task of separating them, since I have never found the two species associated.

T. walkeri is very local in the upper Tennessee region. I found it only in the South Fork Holston at Emmett, Sullivan Co., Tenn., and at Barron, Washington Co., Va. (Walker has it from Barron); and further, I found it in Middle Fork Holston, at Chilhowie, Smyth Co., Va. At the latter place it was not rare.

In addition, the Carnegie Museum has it from Flint River and Hurricane Creek at Gurley and Maysville, Madison Co., Ala. There are also specimens at hand from the type locality.

Type locality: East Fork Stones River, Walterhill, Rutherford Co., Tenn. (cotypes examined).

88. TRUNCILLA CAPSÆFORMIS (Lea), 1834.

Unio capsæformis Lea, '34.—*Unio capsæformis* Lewis, '71.—*Truncilla florentina* and *capsæformis* Ortmann, '12b, p. 359 (anatomy).—*Truncilla capsæformis* Ortmann, '13b, p. 311.—*Truncilla capsæformis* Goodrich, '13, p. 95.—*Truncilla capsæformis* Simpson, '14, p. 29.

The specimen of "*florentina*," of which I have described the anatomy, was actually a *capsæformis*.

Distinguished from the two preceding species by the combination of the following characters: shell rather compressed, with the beaks not much elevated; expansion of the female uniformly dark green, with only small, few, and remote denticles on the margin.

There are differences in the soft parts of *T. turgidula*, *florentina*, *walkeri*, and *capsæformis*, which will be discussed elsewhere.

T. capsæformis is very abundant in the upper Tennessee drainage, all over the region. It is in the Tennessee below Knoxville, in Powell, Clinch, Holston, Nolichucky, Little Pigeon, and goes up, in the French Broad, to Asheville, N. Car. (Walker coll.). It is also in Little Tennessee, at Coytee, Loudon Co., Tenn. (Walker coll.). In the Powell, it has been traced up to Shawanee, Claiborne Co., Tenn.; in the Clinch, to Cedar Bluff, Tazewell Co., Va.; in the North Fork Holston, to Mendota, Washington Co., Va. (also in Big Mocassin Creek); in the South Fork Holston, it is at Pactolus, Sullivan Co., Tenn., but not farther up.

Type locality: Cumberland River.

The above enumeration contains nearly all nominal species ever recorded from the upper Tennessee region. However, there are yet two additional ones, which have not been mentioned:

UNIO ABACUS Haldeman (1824)—Holston River, Tenn.

Pleurobema abacus Simpson, '14, p. 810.

A spurious species, which never has been positively recognized. Specimens under this name in the Lea collection (U. S. Nat. Mus.)

are, as Simpson states, much like "*Pleurobema appressus*," that is to say, *Lexingtonia dolabelloides conradi* (Van.). I have examined these in Washington. Also specimens in the Walker collection, labeled *abacus*, from Flint River, Gurley, Madison Co., Ala., are this.

MARGARITANA QUADRATA Lea (1861)—Eastern Tennessee.

Symphynota quadrata Simpson, '14, p. 487.

The type is lost. This species never has been recognized. I have the suspicion, from description and figure, that it is identical with *Alasmidonta minor* (Lea), 1845.

LIST OF LOCALITIES, AND OF THE NAYAD-FORMS FOUND AT THEM.

The following list is submitted for two reasons: first, to give an idea of the richness of the material upon which this paper is founded; second, to facilitate, for subsequent collectors, the search for certain forms. There will be a time, not far distant, when the fauna of many of the localities will have deteriorated or disappeared in consequence of stream pollution, and thus it is important to know all the localities where a given form has been found. The exact location of all the collecting stations is given on the accompanying map, so that also a change of local geographic nomenclature will not interfere. (See page 523.)

The localities have been arranged according to river systems, beginning in the northwest (Powell), and proceeding downstream and eastward. The smaller streams not belonging to the headwaters, have been placed together at the end of each system. The Tennessee proper stands at the end of the list.

Forms found intergrading at one locality are connected by *braces*. In several instances of well-known and easily recognized species, I have not taken home specimens at certain localities, but only seen them (mostly dead shells). These are marked "*seen*." The record of this fact always was made in the field with actual specimens before me, and is absolutely reliable.

POWELL DRAINAGE.

North Fork Powell River, Big Stone Gap, Wise Co., Va.

Walker coll. (C. C. Adams, Sept. 4, '99).

- | | |
|--|------------------------------|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> | 4. <i>Eurynia nebulosa</i> |
| 2. <i>F. barnesiana bigbyensis</i> | 5. <i>Lampsilis fasciola</i> |
| 3. <i>Medionidus plateolus</i> | |

South Fork Powell River, Big Stone Gap, Wise Co., Va.

* = Walker coll. (Adams, Sept. 4, '99); † = Carnegie Mus.
(Ortmann, May 15 and Sept. 6, '13).

- | | |
|--|-----------------------------------|
| †1. <i>Fusconaia pilaris bursa-pastoris</i> | †7. <i>Alasmidonta minor</i> |
| †2. <i>F. barnesiana</i> } | †8. <i>Strophitus edentulus</i> |
| *†3. <i>F. barnesiana bigbyensis</i> } | †9. <i>Ellipsaria subtenta</i> |
| †4. <i>Lexingtonia dolabelloides conradi</i> | *†10. <i>Toxolasma lividum</i> |
| *†5. <i>Pleurobema oviforme argenteum</i> | *†11. <i>Medionidus plateolus</i> |
| †6. <i>Lasmigona badia</i> | *†12. <i>Eurynia nebulosa</i> |
| | †13. <i>E. vanuxemensis</i> |

Powell River, Olinger, Lee Co., Va.

Walker coll. (Adams, Sept. 5, '99).

- | | |
|---|---------------------------------------|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> | 7. <i>Lasmigona costata</i> |
| 2. <i>F. cuneolus</i> | 8. <i>Alasmidonta marginata</i> |
| 3. <i>F. barnesiana bigbyensis</i> | 9. <i>Ellipsaria subtenta</i> |
| 4. <i>Lexingtonia dolabelloides conradi</i> | 10. <i>Medionidus plateolus</i> |
| 5. <i>Pleurobema oviforme</i> | 11. <i>Eurynia perpurpurea</i> |
| 6. <i>Elliptio dilatatus</i> | 12. <i>E. nebulosa</i> |
| | 13. <i>Lampsilis ovata ventricosa</i> |

Powell River, Dryden, Lee Co., Va.

* = Walker coll. (Adams, Sept. 3, '99); † = Carn. Mus. (Ortmann, Sept. 7, '13).

- | | |
|---|--|
| †1. <i>Fusconaia pilaris bursa-pastoris</i> | †9. <i>Alasmidonta marginata</i> |
| †2. <i>F. barnesiana</i> } | †10. <i>Pegias fabula</i> |
| *†3. <i>F. barnesiana bigbyensis</i> } | †11. <i>Strophitus edentulus</i> |
| *†4. <i>Lexingtonia dolabelloides conradi</i> | *†12. <i>Ellipsaria subtenta</i> |
| †5. <i>Pleurobema oviforme</i> | *†13. <i>Medionidus plateolus</i> |
| *†6. <i>Elliptio dilatatus</i> | *†14. <i>Eurynia nebulosa</i> |
| †7. <i>Lasmigona badia</i> | *†15. <i>E. vanuxemensis</i> |
| *†8. <i>L. costata</i> | †16. <i>Lampsilis ovata ventricosa</i> |
| | *†17. <i>L. fasciola</i> |

Cane Creek, Pennington Gap, Lee Co., Va.

Walker coll.

- | | |
|--|-------------------------------|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> | 2. <i>Pleurobema oviforme</i> |
|--|-------------------------------|

Puckell Creek, Pennington Gap, Lee Co., Va.

Walker coll.

- | | |
|---|-------------------------------|
| 1. <i>Fusconaia cuneolus</i> | 3. <i>Pleurobema oviforme</i> |
| 2. <i>Lexingtonia dolabelloides conradi</i> | |

Wallen Creek, Lee Co., Va. (near Jonesville).

* = Walker coll.; † = Carn. Mus. (from G. H. Clapp).

- | | |
|--|---------------------------------|
| *1. <i>Fusconaia barnesiana bigbyensis</i> | *4. <i>Medionidus plateolus</i> |
| †2. <i>Elliptio dilatatus</i> | †5. <i>Eurynia nebulosa</i> |
| *3. <i>Pegias fabula</i> | |

Powell River, Lytton Mill, Pennington Gap, Lee Co., Va.

Walker coll. (Adams, Sept. 1, '99).

- | | |
|---|----------------------------------|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> | 8. <i>Lasmigona costata</i> |
| 2. <i>F. cor analoga</i> | 9. <i>Ellipsaria fasciolaris</i> |
| 3. <i>F. barnesiana bigbyensis</i> | 10. <i>Nephronaias pectorosa</i> |
| 4. <i>Quadrula cylindrica strigillata</i> | 11. <i>Eurynia nebulosa</i> |
| 5. <i>Lexingtonia dolabelloides conradi</i> | 12. <i>E. vanuxemensis</i> |
| 6. <i>Pleurobema oviforme</i> | 13. <i>Lampsilis fasciola</i> |
| 7. <i>Elliptio dilatatus</i> | 14. <i>Truncilla haysiana</i> |

Powell River, Jonesville, Lee Co., Va.

* = Walker coll.; † = Carn. Mus. (Hartman coll.).

- | | |
|---|--------------------------------|
| *1. <i>Fusconaia pilaris bursa-pastoris</i> | *4. <i>Ellipsaria subtenta</i> |
| *2. <i>Pleurobema oviforme</i> | *5. <i>Toxolasma lividum</i> |
| *3. <i>Elliptio niger</i> | *†6. <i>Lemiox rimosus</i> |

Powell River, Rose Hill, Lee Co., Va.

Walker coll. (Adams, Aug. 5, '01).

- | | |
|--|---------------------------------|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> | 8. <i>Nephronaias pectorosa</i> |
| 2. <i>F. cor analoga</i> | 9. <i>Lemiox rimosus</i> |
| 3. <i>F. barnesiana bigbyensis</i> | 10. <i>Medionidus plateolus</i> |
| 4. <i>Pleurobema oviforme</i> | 11. <i>Eurynia nebulosa</i> |
| 5. <i>Elliptio dilatatus</i> | 12. <i>Lampsilis fasciola</i> |
| 6. <i>Alasmidonta marginata</i> | 13. <i>Truncilla interrupta</i> |
| 7. <i>Ellipsaria fasciolaris</i> | |

Powell River, Shawanee, Claiborne Co., Tenn.

Walker coll. (Adams, Aug. 31, '99).

- | | |
|--|-------------------------------------|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> } | 14. <i>Nephronaias pectorosa</i> |
| 2. <i>F. pilaris lesueuriana</i> } | 15. <i>Toxolasma lividum</i> |
| 3. <i>F. cuneolus</i> | 16. <i>Medionidus plateolus</i> |
| 4. <i>F. cor analoga</i> | 17. <i>Eurynia nebulosa</i> |
| 5. <i>F. barnesiana bigbyensis</i> | 18. <i>Lampsilis ovata</i> |
| 6. <i>Amblema plicata costata</i> | 19. <i>L. ovata ventricosa</i> |
| 7. <i>Pleurobema oviforme</i> } | 20. <i>L. fasciola</i> |
| 8. <i>P. oviforme argenteum</i> } | 21. <i>Truncilla triquetra</i> |
| 9. <i>Elliptio niger</i> | 22. <i>T. interrupta</i> |
| 10. <i>E. dilatatus</i> | 23. <i>T. haysiana</i> |
| 11. <i>Ellipsaria subtenta</i> | 24. <i>T. torulosa gubernaculum</i> |
| 12. <i>Dromus dromas caperatus</i> | 25. <i>T. capsæformis</i> |
| 13. <i>Nephronaias ligamentina gibba</i> | |

Powell River, Bryant Shoals, Claiborne Co., Tenn.

Walker coll. (Adams, Aug. 30, '99).

- | | |
|---|--|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> | 12. <i>Alasmidonta marginata</i> |
| 2. <i>F. cor analoga</i> | 13. <i>Ellipsaria fasciolaris</i> |
| 3. <i>Amblema plicata costata</i> | 14. <i>E. subtenta</i> |
| 4. <i>Quadrula pustulosa</i> | 15. <i>Dromus dromas caperatus</i> |
| 5. <i>Quadrula cylindrica strigillata</i> | 16. <i>Nephronaias ligamentina gibba</i> |
| 6. <i>Plethobasus cyphus</i> | 17. <i>N. pectorosa</i> |
| 7. <i>Lexingtonia dolabelloides conradi</i> | 18. <i>Lemiox rimosus</i> |
| 8. <i>Pleurobema oviforme</i> } | 19. <i>Medionidus plateolus</i> |
| 9. <i>P. oviforme argenteum</i> } | 20. <i>Eurynia nebulosa</i> |
| 10. <i>Elliptio dilatatus</i> | 21. <i>Lampsilis fasciola</i> |
| 11. <i>Lasmigona costata</i> | 22. <i>Truncilla interrupta</i> |
| | 23. <i>T. capsæformis</i> |

Powell River, Combs, Claiborne Co., Tenn.

Carn. Mus. (Ortmann, Sept. 12, '13 and Sept. 13, '15).

- | | |
|---|--|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> | 12. <i>Elliptio dilatatus</i> |
| 2. <i>F. pilaris lesueuriana</i> | 13. <i>Lasmigona costata</i> |
| 3. <i>F. cuneolus</i> | 14. <i>Alasmidonta marginata</i> |
| 4. <i>F. cor analoga</i> | 15. <i>Strophitus edentulus</i> |
| 5. <i>F. barnesiana bigbyensis</i> | 16. <i>Ellipsaria fasciolaris</i> |
| 6. <i>Amblema plicata costata</i> | 17. <i>E. subtenta</i> |
| 7. <i>Quadrula cylindrica</i> | 18. <i>Dromus droma caperatus</i> |
| 8. <i>Plethobasus cyphus</i> | 20. <i>Nephronaias pectorosa</i> |
| 9. <i>Lexingtonia dolabelloides conradi</i> | 19. <i>Nephronaias ligamentina gibba</i> |
| 10. <i>Pleurobema oviforme</i> } | 21. <i>Paraptera fragilis</i> |
| 11. <i>P. oviforme argenteum</i> } | 22. <i>Proptera alata</i> |
| | 23. <i>Lemiox rimosus</i> |

- | | |
|----------------------------------|-------------------------------------|
| 24. <i>Medionidus plateolus</i> | 31. <i>L. fasciola</i> |
| 25. <i>Eurynia fabalis</i> | 32. <i>Truncilla triquetra</i> |
| 26. <i>E. nebulosa</i> | 33. <i>T. interrupta</i> |
| 27. <i>E. vanuxemensis</i> | 34. <i>T. haysiana</i> |
| 28. <i>E. recta</i> | 35. <i>T. lewisi</i> |
| 29. <i>Lampsilis ovata</i> } | 36. <i>T. torulosa gubernaculum</i> |
| 30. <i>L. ovata ventricosa</i> } | 37. <i>T. capsaeformis</i> |

Powell River, Green's Ford, Union Co., Tenn.

Walker coll. (Adams, Aug. 23, '99).

(Adams says: Campbell Co., Walker: Claiborne Co.; the locality is, where the three counties meet, and the ford is, according to map—sheet Maynardville—rather in Union Co.)

- | | |
|--|-----------------------------------|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> | 10. <i>Strophitus edentulus</i> |
| 2. <i>F. pilaris lesueuriana</i> | 11. <i>Ellipsaria fasciolaris</i> |
| 3. <i>F. cuneolus</i> | 12. <i>E. subtenta</i> |
| 4. <i>F. barnesiana</i> | 13. <i>Toxolasma lividum</i> |
| 5. <i>Amblema plicata costata</i> | 14. <i>Medionidus plateolus</i> |
| 6. <i>Quadrula cylindrica</i> | 15. <i>Eurynia fabalis</i> |
| 7. <i>Elliptio niger</i> | 16. <i>E. nebulosa</i> |
| 8. <i>E. dilatatus</i> | 17. <i>Truncilla interrupta</i> |
| 9. <i>Lasmigona costata</i> | 18. <i>T. capsaeformis</i> |

Powell River, Powell River P. O., Campbell Co., Tenn.

Walker coll. (Adams, Aug. 23, '99).

- | | |
|-----------------------------------|-------------------------------|
| 1. <i>Amblema plicata costata</i> | 5. <i>Eurynia fabalis</i> |
| 2. <i>Elliptio dilatatus</i> | 6. <i>Truncilla triquetra</i> |
| 3. <i>Lasmigona costata</i> | 7. <i>T. capsaeformis</i> |
| 4. <i>Ellipsaria subtenta</i> | |

CLINCH DRAINAGE.

North Fork Clinch River, Tazewell, Tazewell Co., Va.

Walker coll. (Adams).

- | | |
|-----------------------------|----------------------------|
| 1. <i>Alasmidonta minor</i> | 2. <i>Eurynia nebulosa</i> |
|-----------------------------|----------------------------|

Clinch River, Tazewell, Tazewell Co., Va.

Carn. Mus. (Ortmann, Sept. 19, '12).

- | | |
|---|---------------------------|
| 1. <i>Fusconaia barnesiana bigbyensis</i> | 2. <i>Lasmigona badia</i> |
|---|---------------------------|

Clinch River, Cedar Bluff, Tazewell Co., Va.

Carn. Mus. (Ortmann, Sept. 20, '12, and May 11, '13).

- | | |
|---|---------------------------------------|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> | 10. <i>Alasmidonta minor</i> |
| 2. <i>F. barnesiana bigbyensis</i> | 11. <i>Strophitus edentulus</i> |
| 3. <i>Quadrula cylindrica strigillata</i> | 12. <i>Ellipsaria subtenta</i> |
| 4. <i>Lexingtonia dolabelloides conradi</i> | 13. <i>Medionidus plateolus</i> |
| 5. <i>Pleurobema oviforme</i> } | 14. <i>Eurynia perpurpurea</i> |
| 6. <i>P. oviforme argenteum</i> } | 15. <i>E. nebulosa</i> |
| 7. <i>Elliptio dilatatus</i> | 16. <i>Lampsilis ovata ventricosa</i> |
| 8. <i>Lasmigona badia</i> | 17. <i>L. fasciola</i> |
| 9. <i>L. costata</i> | 18. <i>Truncilla capsaeformis</i> |

Clinch River, Richland, Tazewell Co., Va.

Carn. Mus. (Ortmann, Sept. 20, '12).

- | | |
|---|---------------------------------------|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> | 10. <i>L. costata</i> |
| 2. <i>F. barnesiana</i> } | 11. <i>Alasmidonta minor</i> |
| 3. <i>F. barnesiana bigbyensis</i> } | 12. <i>A. marginata</i> |
| 4. <i>Quadrula cylindrica strigillata</i> | 13. <i>Strophitus edentulus</i> |
| 5. <i>Lexingtonia dolabelloides conradi</i> | 14. <i>Ellipsaria subtenta</i> |
| 6. <i>Pleurobema oviforme</i> } | 15. <i>Medionidus plateolus</i> |
| 7. <i>P. oviforme argenteum</i> } | 16. <i>Eurynia perpurpurea</i> |
| 8. <i>Elliptio dilatus</i> | 17. <i>E. nebulosa</i> |
| 9. <i>Lasmigona badia</i> | 18. <i>Lampsilis ovata ventricosa</i> |
| | 19. <i>L. fasciola</i> |

Clinch River, Raven, Tazewell Co., Va.

Carn. Mus. (Ortmann, Sept. 21, '12).

- | | |
|---|---------------------------------------|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> | 9. <i>Strophitus edentulus</i> |
| 2. <i>F. barnesiana bigbyensis</i> | 10. <i>Ellipsaria subtenta</i> |
| 3. <i>Quadrula cylindrica strigillata</i> | 11. <i>Medionidus plateolus</i> |
| 4. <i>Lexingtonia dolabelloides conradi</i> | 12. <i>Eurynia perpurpurea</i> |
| 5. <i>Pleurobema oviforme</i> } | 13. <i>E. nebulosa</i> |
| 6. <i>P. oviforme argenteum</i> } | 14. <i>Lampsilis ovata ventricosa</i> |
| 7. <i>Elliptio dilatatus</i> | 15. <i>L. fasciola</i> |
| 8. <i>Lasmigona costata</i> | 16. <i>Truncilla haysiana</i> |
| | 17. <i>T. capsaeformis</i> |

Clinch River, Cleveland, Russell Co., Va.

* = Walker coll. (Adams, Aug., '99); † = Carn. Mus. (Ortmann, May 13, '13).

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|---|------------------------------------|
| †1. <i>Fusconaia pilaris bursa-pastoris</i> | †3. <i>Amblema plicata costata</i> |
| *†2. <i>F. cor analoga</i> | *†4. <i>Quadrula intermedia</i> |

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|---|--|
| †5. <i>Q. cylindrica strigillata</i> | †15. <i>Strophitus edentulus</i> |
| *†6. <i>Lexingtonia dolabelloides conradi</i> | *†16. <i>Ellipsaria fasciolaris</i> |
| †7. <i>Pleurobema obliquum coccineum</i> | *†17. <i>E. subtenta</i> |
| †8. <i>P. oviforme</i> | *†18. <i>Nephronaias pectorosa</i> |
| †9. <i>P. oviforme argenteum</i> | *†19. <i>Medionidus plateolus</i> |
| *†10. <i>Elliptio dilatatus</i> | *†20. <i>Eurynia fabalis</i> |
| *†11. <i>Lastena lata</i> | *†21. <i>E. perpurpurea</i> |
| *†12. <i>Lasmigona costata</i> | †22. <i>E. nebulosa</i> |
| †13. <i>Alasmidonta minor</i> | †23. <i>Lampsilis ovata ventricosa</i> |
| †14. <i>Alasmidonta marginata</i> | *†24. <i>L. fasciola</i> |
| | *†25. <i>Truncilla capsæformis</i> |

Clinch River, Fink, Russell Co., Va.

Carn. Mus. (Ortmann, May 12, '13).

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|--|---------------------------------------|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> | 9. <i>Alasmidonta marginata</i> |
| 2. <i>F. cor analoga</i> | 10. <i>Ellipsaria fasciolaris</i> |
| 3. <i>F. barnesiana bigbyensis</i> | 11. <i>Nephronaias pectorosa</i> |
| 4. <i>Amblema plicata costata</i> | 12. <i>Medionidus plateolus</i> |
| 5. <i>Quadrula cylindrica strigillata</i> | 13. <i>Eurynia nebulosa</i> |
| 6. <i>Pleurobema oviforme argenteum</i> | 14. <i>Lampsilis ovata ventricosa</i> |
| 7. <i>Elliptio dilatatus</i> | 15. <i>L. fasciola</i> |
| 8. <i>Lasmigona costata</i> | 16. <i>Truncilla capsæformis</i> |

Clinch River, St. Paul, Wise Co., Va.

* = Walker coll. (Adams, Aug. 8, '99); † = Carn. Mus. (Ortmann, May 14, '13).

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|--|---|
| †1. <i>Fusconaia pilaris bursa-pastoris</i> | *†13. <i>Ellipsaria fasciolaris</i> |
| †2. <i>F. cor analoga</i> | *†14. <i>Ellipsaria subtenta</i> |
| †3. <i>F. barnesiana bigbyensis</i> | †15. <i>Nephronaias ligamentina gibba</i> |
| *†4. <i>Amblema plicata costata</i> | *†16. <i>N. pectorosa</i> |
| †5. <i>Lexingtonia dolabelloides conradi</i> | †17. <i>Lemiox rimosus</i> |
| †6. <i>Pleurobema oviforme argenteum</i> | *†18. <i>Medionidus plateolus</i> |
| *†7. <i>Elliptio dilatatus</i> | †19. <i>Eurynia fabalis</i> |
| †8. <i>Lastena lata</i> | †20. <i>E. perpurpurea</i> |
| *†9. <i>Lasmigona costata</i> | *†21. <i>E. nebulosa</i> |
| †10. <i>Alasmidonta minor</i> | †22. <i>E. recta</i> |
| *†11. <i>A. marginata</i> | †23. <i>Lampsilis ovata ventricosa</i> |
| †12. <i>Strophitus edentulus</i> | *†24. <i>L. fasciola</i> |
| | *†25. <i>Truncilla capsæformis</i> |

Clinch River, Dungannon, Scott Co., Va.

Walker coll. (Adams, Aug. 11, '99).

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|-----------------------------------|---|
| 1. <i>Amblema plicata costata</i> | 2. <i>Truncilla torulosa gubernaculum</i> |
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Clinch River, Clinchport, Scott Co., Va.

*=Walker coll. (Adams, Aug., '99); †=Carn. Mus. (Ortmann, Sept. 8, '13).

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|---|--|
| *†1. <i>Fusconaia pilaris bursa-pastoris</i> | *†18. <i>Alasmidonta marginata</i> |
| *†2. <i>F. pilaris lesueuriana</i> | *†19. <i>Ellipsaria fasciolaris</i> |
| †3. <i>F. cuneolus</i> | †20. <i>E. subtenta</i> |
| *†4. <i>F. cor analoga</i> | *†21. <i>Nephronaias ligamentina gibba</i> |
| †5. <i>F. barnesiana bigbyensis</i> | *†22. <i>N. pectorosa</i> |
| *†6. <i>Amblema plicata costata</i> | *†23. <i>Proptera alata</i> |
| *7. <i>Quadrula intermedia</i> | *†24. <i>Medionidus plateolus</i> |
| †8. <i>Q. cylindrica</i> | †25. <i>Eurynia perpurpurea</i> |
| *9. <i>Rotundaria tuberculata</i> | †26. <i>E. nebulosa</i> |
| †10. <i>Plethobasus cyphus</i> | †27. <i>E. recta</i> |
| †11. <i>Lexingtonia dolabelloides conradi</i> | †28. <i>Lampsilis ovata</i> |
| †12. <i>Pleurobema obliquum coccineum</i> | *†29. <i>L. ovata ventricosa</i> |
| †13. <i>P. oviforme</i> | *†30. <i>L. fasciola</i> |
| *†14. <i>Elliptio niger</i> | †31. <i>Truncilla triquetra</i> |
| *†15. <i>E. dilatatus</i> | *†32. <i>T. interrupta</i> |
| *16. <i>Lastena lata</i> | *†33. <i>T. torulosa gubernaculum</i> |
| *†17. <i>Lasmigona costata</i> | *†34. <i>T. capsæformis</i> |

Clinch River, Speer's Ferry, Scott Co., Va.

Carn. Mus. (Ortmann, July 8, '13).

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|--|---------------------------------------|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> | 14. <i>Toxolasma lividum</i> |
| 2. <i>F. cuneolus</i> | 15. <i>Medionidus plateolus</i> |
| 3. <i>F. cor analoga</i> | 16. <i>Eurynia fabalis</i> |
| 4. <i>Amblema plicata costata</i> | 17. <i>E. trabalis</i> |
| 5. <i>Quadrula cylindrica</i> | 18. <i>E. perpurpurea</i> |
| 6. <i>Rotundaria tuberculata</i> | 19. <i>E. nebulosa</i> |
| 7. <i>Pleurobema oviforme argenteum</i> | 20. <i>E. vanuxemensis</i> |
| 8. <i>Elliptio dilatatus</i> | 21. <i>Lampsilis ovata ventricosa</i> |
| 9. <i>Lasmigona costata</i> | 22. <i>Truncilla triquetra</i> |
| 10. <i>Alasmidonta minor</i> | 23. <i>T. interrupta</i> |
| 11. <i>A. marginata</i> | 24. <i>T. lenior</i> |
| 12. <i>Ellipsaria fasciolaris</i> | 25. <i>T. capsæformis</i> |
| 13. <i>Nephronaias pectorosa</i> (seen) | |

Clinch River, Church Ford, Scott Co., Va.

Walker coll.

1. *Fusconaia cor analoga*

Clinch River, Horton Ford, Hancock Co., Tenn.

Walker coll. (Adams, Aug. 14, '99).

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|--|---|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> | 5. <i>Nephronaias ligamentina gibba</i> |
| 2. <i>F. cuneolus</i> | 6. <i>N. pectorosa</i> |
| 3. <i>Rotundaria tuberculata</i> | 7. <i>Truncilla triquetra</i> |
| 4. <i>Lasmigona costata</i> | 8. <i>T. capsæformis</i> |

Clinch River, Kyle Ford, Hancock Co., Tenn.

Walker coll.

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|--|---|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> | 6. <i>Elliptio dilatatus</i> |
| 2. <i>F. pilaris lesueuriana</i> | 7. <i>Ellipsaria subtenta</i> |
| 3. <i>F. barnesiana</i> | 8. <i>Medionidus plateolus</i> |
| 4. <i>Pleurobema oviforme</i> } | 9. <i>Truncillatorulosagubernaculum</i> |
| 5. <i>T. oviforme argenteum</i> } | |

Clinch River, Sneedville, Hancock Co. Tenn. ("between Kyle Ford and Sneedville").

Walker coll. (Adams, Aug. 16, '99).

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|--|-------------------------------|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> | 4. <i>Elliptio dilatatus</i> |
| 2. <i>F. cor analoga</i> | 5. <i>Ellipsaria subtenta</i> |
| 3. <i>Plethobasus cyphus</i> | |

Clinch River, Oakman, Grainger Co., Tenn.

Carn. Mus. (Ortmann, May 25, '15; Sept. 14, '15).

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|--|-------------------------------------|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> | 16. <i>Nephronaias pectorosa</i> |
| 2. <i>F. cuneolus</i> | 17. <i>Amygdalonaias truncata</i> |
| 3. <i>Amblema plicata costata</i> | 18. <i>Proptera alata</i> |
| 4. <i>Rotundaria tuberculata</i> | 19. <i>Medionidus plateolus</i> |
| 5. <i>Plethobasus cyphus</i> | 20. <i>Eurynia nebulosa</i> |
| 6. <i>Pleurobema obliquum rubrum</i> | 21. <i>E. vanuxemensis</i> |
| 7. <i>Elliptio niger</i> | 22. <i>E. recta</i> |
| 8. <i>E. dilatatus</i> | 23. <i>Lampsilis ovata</i> } |
| 9. <i>Lastena lata</i> | 24. <i>L. ovata ventricosa</i> } |
| 10. <i>Lasmigona costata</i> | 25. <i>L. fasciola</i> |
| 11. <i>Alasmidonta marginata</i> | 26. <i>Truncilla triquetra</i> |
| 12. <i>Strophitus edentulus</i> | 27. <i>T. arcæformis</i> |
| 13. <i>Ellipsaria fasciolaris</i> | 28. <i>T. interrupta</i> |
| 14. <i>Cyprogenia stegaria</i> | 29. <i>T. torulosa gubernaculum</i> |
| 15. <i>Nephronaias ligamentina gibba</i> | 30. <i>T. capsæformis</i> |

Clinch River, Clinch River Station, Claiborne Co., Tenn.

Carn. Mus. (Ortmann, Sept. 11, '13).

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|---|--|
| 1. <i>Cumberlandia monodonta</i> | 19. <i>Dromus dromas caperatus</i> |
| 2. <i>Fusconaia pilaris bursa-pastoris</i> | 20. <i>Nephronaias ligamentina gibba</i> |
| 3. <i>F. cuneolus</i> | 21. <i>N. pectorosa</i> |
| 4. <i>F. cor analoga</i> | 22. <i>Amygdaloniaias truncata</i> |
| 5. <i>Amblema plicata costata</i> | 23. <i>Paraptera fragilis</i> |
| 6. <i>Quadrula cylindrica</i> | 24. <i>Proptera alata</i> |
| 7. <i>Rotundaria tuberculata</i> | 25. <i>Medionidus plateolus</i> |
| 8. <i>Plethobasus cyphus</i> | 26. <i>Eurynia fabalis</i> |
| 9. <i>Lexingtonia dolabelloides conradi</i> | 27. <i>E. nebulosa</i> |
| 10. <i>Pleurobema obliquum rubrum</i> | 28. <i>E. recta</i> |
| 11. <i>Elliptio niger</i> | 29. <i>Lampsilis ovata</i> |
| 12. <i>E. dilatatus</i> | 30. <i>L. ovata ventricosa</i> |
| 13. <i>Lasmigona costata</i> | 31. <i>L. fasciola</i> |
| 14. <i>Alasmidonta marginata</i> | 32. <i>Truncilla triquetra</i> |
| 15. <i>Strophitus edentulus</i> | 33. <i>T. arcæformis</i> |
| 16. <i>Ellipsaria fasciolaris</i> | 34. <i>T. interrupta</i> |
| 17. <i>E. subtenta</i> | 35. <i>T. haysiana</i> |
| 18. <i>Cyprogenia stegaria</i> | 36. <i>T. torulosa gubernaculum</i> |
| | 37. <i>T. capsæformis</i> |

Clinch River, Black Fox Ford, Union Co., Tenn.

* = Walker coll. (Adams, Aug. 19, '99); † = Carn. Mus. (Ortmann, Sept. 15, '15).

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|--|---|
| *†1. <i>Fusconaia pilaris bursa-pastoris</i> | †16. <i>Nephronaias ligamentina gibba</i> |
| †2. <i>F. pilaris lesueuriana</i> | †17. <i>N. pectorosa</i> |
| *†3. <i>F. cuneolus</i> | *†18. <i>Amygdaloniaias truncata</i> |
| †4. <i>Amblema plicata costata</i> | 19. <i>Proptera alata</i> (seen) |
| 5. <i>Rotundaria tuberculata</i> (seen) | †20. <i>Medionidus plateolus</i> |
| †6. <i>Plethobasus cyphus</i> | †21. <i>Eurynia nebulosa</i> |
| †7. <i>Pleurobema obliquum catillus</i> | 22. <i>E. recta</i> (seen) |
| *†8. <i>P. obliquum rubrum</i> | †23. <i>Lampsilis ovata</i> |
| 9. <i>Elliptio dilatatus</i> (seen) | *24. <i>L. ovata ventricosa</i> |
| *10. <i>Lasmigona costata</i> (seen) | †25. <i>L. fasciola</i> |
| *†11. <i>Alasmidonta marginata</i> | *†26. <i>Truncilla triquetra</i> |
| 12. <i>Strophitus edentulus</i> (seen) | *†27. <i>T. interrupta</i> |
| †13. <i>Ellipsaria fasciolaris</i> | *†28. <i>T. haysiana</i> |
| *14. <i>E. subtenta</i> | *†29. <i>T. torulosa gubernaculum</i> |
| †15. <i>Cyprogenia stegaria</i> | *†30. <i>T. capsæformis</i> |

Clinch River, Walker's Ford, Union Co., Tenn.

Walker coll.

- 1.
- Fusconaia barnesiana*

Clinch River, Needham Ford, Union Co., Tenn.

Walker coll. (Adams, Aug. 19, '99).

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|--|--|
| 1. <i>Cumberlandia monodonta</i> | 14. <i>Alasmidonta marginata</i> |
| 2. <i>Fusconaia pilaris bursa-pastoris</i> } | 15. <i>Strophitus edentulus</i> |
| 3. <i>F. pilaris lesueuriana</i> | 16. <i>Ellipsaria fasciolaris</i> |
| 4. <i>F. cor</i> | 17. <i>Cyprogenia stegaria</i> |
| 5. <i>F. cor analoga</i> | 18. <i>Dromus dromas caperatus</i> |
| 6. <i>Rotundaria tuberculata</i> | 19. <i>Nephronaias ligamentina gibba</i> |
| 7. <i>Plethobasus cyphus</i> | 20. <i>N. pectorosa</i> |
| 8. <i>Pleurobema obliquum</i> } | 21. <i>Paraptera leptodon</i> |
| 9. <i>P. obliquum coccineum</i> } | 22. <i>Proptera alata</i> |
| 10. <i>P. obliquum rubrum</i> | 23. <i>Eurynia recta</i> |
| 11. <i>Elliptio niger</i> | 24. <i>Lampsilis ovata</i> |
| 12. <i>E. dilatatus</i> | 25. <i>L. fasciola</i> |
| 13. <i>Lasmigona costata</i> | 26. <i>Truncilla interrupta</i> |

Clinch River, Kelly Ford, Union Co., Tenn.

Walker coll. (Adams, Aug. 20, '99) ("between Kelly and Sharp's Ford").

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|----------------------------------|--|
| 1. <i>Cumberlandia monodonta</i> | 2. <i>Truncilla torulosagubernaculum</i> |
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Clinch River, below Agee, Campbell Co., Tenn.

Walker coll. (Adams, Aug. 24, '99) ("Agee to Offutt").

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|---|--|
| 1. <i>Cumberlandia monodonta</i> | 9. <i>Elliptio niger</i> |
| 2. <i>Fusconaia pilaris lesueuriana</i> | 10. <i>E. dilatatus</i> |
| 3. <i>Quadrula cylindrica</i> | 11. <i>Ellipsaria fasciolaris</i> |
| 4. <i>Rotundaria tuberculata</i> | 12. <i>Obliquaria reflexa</i> |
| 5. <i>Plethobasus cyphus</i> | 13. <i>Cyprogenia stegaria</i> |
| 6. <i>Lexingtonia dolabelloides</i> | 14. <i>Dromus dromas caperatus</i> |
| 7. <i>Pleurobema obliquum</i> | 15. <i>Nephronaias ligamentina gibba</i> |
| 8. <i>P. obliquum rubrum</i> | 16. <i>Eurynia recta</i> |

Clinch River, Offutt, Anderson Co., Tenn.

Carn. Mus. (Ortmann, Sept. 1, '14).

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|--|--|
| 1. <i>Cumberlandia monodonta</i> | 13. <i>Lasmigona costata</i> |
| 2. <i>Fusconaia pilaris bursa-pastoris</i> } | 14. <i>Ellipsaria fasciolaris</i> |
| 3. <i>F. pilaris lesueuriana</i> | 15. <i>Cyprogenia stegaria</i> |
| 4. <i>F. cuneolus appressa</i> | 16. <i>Dromus dromas caperatus</i> |
| 5. <i>Amblema plicata costata</i> | 17. <i>Nephronaias ligamentina gibba</i> |
| 6. <i>Quadrula pustulosa</i> | 18. <i>Plagiola lineolata</i> |
| 7. <i>Rotundaria tuberculata</i> | 19. <i>Proptera alata</i> |
| 8. <i>Plethobasus cyphus</i> | 20. <i>Eurynia recta</i> |
| 9. <i>Pleurobema obliquum</i> | 21. <i>Lampsilis ovata</i> |
| 10. <i>P. obliquum rubrum</i> | 22. <i>L. fasciola</i> (seen) |
| 11. <i>Elliptio niger</i> | 23. <i>L. orbiculata</i> |
| 12. <i>E. dilatatus</i> | |

Clinch River, Clinton, Anderson Co., Tenn. (Moore Ferry).

* = Walker coll. (Adams, Aug. 25, '99) ("between Offutt and Clinton"); † = Carn. Mus. (Ortmann, Sept. 7, '14); (no. 42: Hartman coll.).

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|--|--|
| 1. <i>Cumberlandia monodonta</i>
(seen) | *†23. <i>Alasmidonta marginata</i> |
| *2. <i>Fusconaia pilaris</i> | †24. <i>Strophitus edentulus</i> |
| *†3. <i>F. pilaris lesueuriana</i> } | *†25. <i>Ellipsaria fasciolaris</i> |
| †4. <i>F. pilaris bursa-pastoris</i> } | †26. <i>E. subtenta</i> |
| †5. <i>F. cuneolus</i> } | †27. <i>Obliquaria reflexa</i> |
| *†6. <i>F. cuneolus appressa</i> } | *†28. <i>Cyprogenia stegaria</i> |
| †7. <i>F. barnesiana</i> | †29. <i>Dromus dromas caperatus</i> |
| †8. <i>Amblema plicata costata</i> | †30. <i>Obovaria retusa</i> |
| †9. <i>Quadrula pustulosa</i> | *†31. <i>Nephronaias ligamentina gibba</i> |
| *†10. <i>Q. cylindrica</i> | *†32. <i>Amygdalonia truncata</i> |
| *†11. <i>Rotundaria tuberculata</i> | 33. <i>Proptera alata</i> (seen) |
| †12. <i>Plethobasus cyphus</i> | †34. <i>Lemiox rimosus</i> |
| †13. <i>Lexingtonia dolabelloides</i> } | †35. <i>Eurynia vanuxemensis</i> |
| †14. <i>L. dolabelloides conradi</i> } | *†36. <i>E. recta</i> |
| *†15. <i>Pleurobema obliquum</i> } | *†37. <i>Lampsilis ovata</i> |
| †16. <i>P. obliquum cordatum</i> } | †38. <i>L. ovata ventricosa</i> |
| *†17. <i>P. obliquum rubrum</i> | †39. <i>L. fasciola</i> |
| †18. <i>P. oviforme</i> | *†40. <i>Truncilla triquetra</i> |
| *†19. <i>Elliptio niger</i> | †41. <i>T. haysiana</i> |
| *†20. <i>E. dilatatus</i> | †42. <i>T. stewardsoni</i> (Hartm. coll.) |
| †21. <i>Lastena lata</i> | †43. <i>T. propinqua</i> |
| *22. <i>Lasmigona costata</i> (seen) | †44. <i>T. capsaeformis</i> |

Clinch River, Edgemoor, Anderson Co., Tenn.

Carn. Mus. (Ortmann, Sept. 8, '14; Sept. 17, '15).

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|---------------------------------------|--|
| 1. <i>Cumberlandia monodonta</i> | 16. <i>P. obliquum rubrum</i> |
| 2. <i>Fusconaia pilaris</i> } | 17. <i>P. oviforme holstonense</i> |
| 3. <i>F. pilaris lesueuriana</i> } | 18. <i>Elliptio niger</i> |
| 4. <i>F. pilaris bursa-pastoris</i> } | 19. <i>E. dilatatus</i> |
| 5. <i>F. cor</i> | 20. <i>Lastena lata</i> |
| 6. <i>F. barnesiana</i> } | 21. <i>Lasmigona costata</i> |
| 7. <i>F. barnesiana tumescens</i> } | 22. <i>Alasmidonta marginata</i> |
| 8. <i>Quadrula pustulosa</i> | 23. <i>Strophitus edentulus</i> |
| 9. <i>Q. cylindrica</i> | 24. <i>Ellipsaria fasciolaris</i> |
| 10. <i>Rotundaria tuberculata</i> | 25. <i>Obliquaria reflexa</i> |
| 11. <i>Plethobasus cooperianus</i> | 26. <i>Cyprogenia stegaria</i> |
| 12. <i>P. cyphus</i> | 27. <i>Dromus dromas caperatus</i> |
| 13. <i>Pleurobema obliquum</i> } | 28. <i>Nephronaias ligamentina gibba</i> |
| 14. <i>P. obliquum cordatum</i> } | 29. <i>Amygdalonia truncata</i> |
| 15. <i>P. obliquum catillus</i> } | 30. <i>Paraptera leptodon</i> |

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|----------------------------------|--------------------------------|
| 31. <i>P. fragilis</i> | 37. <i>Truncilla triquetra</i> |
| 32. <i>Proptera alata</i> | 38. <i>T. interrupta</i> |
| 33. <i>Eurynia recta</i> | 39. <i>T. haysiana</i> |
| 34. <i>Lampsilis ovata</i> } | 40. <i>T. propinqua</i> |
| 35. <i>L. ovata ventricosa</i> } | 41. <i>T. capsæformis</i> |
| 36. <i>L. fasciola</i> | |

Clinch River, Solway, Knox Co., Tenn.

Carn. Mus. (Ortmann, Sept. 12, '14).

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|---------------------------------------|--|
| 1. <i>Cumberlandia monodonta</i> | 18. <i>Elliptio dilatatus</i> |
| 2. <i>Fusconaia pilaris</i> } | 19. <i>Strophitus edentulus</i> |
| 3. <i>F. pilaris lesueuriana</i> } | 20. <i>Obliquaria reflexa</i> |
| 4. <i>F. pilaris bursa-pastoris</i> } | 21. <i>Cyprogenia stegaria</i> |
| 5. <i>F. cuneolus appressa</i> | 22. <i>Dromus dromas caperatus</i> |
| 6. <i>F. barnesiana bigbyensis</i> | 23. <i>Nephronaias ligamentina gibba</i> |
| 7. <i>Amblema plicata costata</i> | 24. <i>Amygdaloniais truncata</i> |
| 8. <i>Quadrula pustulosa</i> | 25. <i>Paraptera fragilis</i> (seen) |
| 9. <i>Q. cylindrica</i> (seen) | 26. <i>Proptera alata</i> |
| 10. <i>Rotundaria tuberculata</i> | 27. <i>Eurynia nebulosa</i> |
| 11. <i>Plethobasus cyphus</i> | 28. <i>E. recta</i> |
| 12. <i>Lexingtonia dolabelloides</i> | 29. <i>Lampsilis ovata</i> } |
| 13. <i>Pleurobema obliquum</i> } | 30. <i>L. ovata ventricosa</i> } |
| 14. <i>P. obliquum cordatum</i> } | 31. <i>L. orbiculata</i> |
| 15. <i>P. obliquum coccineum</i> } | 32. <i>Truncilla triquetra</i> |
| 16. <i>P. obliquum rubrum</i> } | 33. <i>T. haysiana</i> |
| 17. <i>Elliptio niger</i> | 34. <i>T. capsæformis</i> |

Clinch River, Patton's Ferry, Roane Co., Tenn.

(According to Pilsbry & Rhoads.)

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|--------------------------------------|--|
| 1. <i>Fusconaia pilaris</i> | 9. <i>Elliptio dilatatus</i> |
| 2. <i>F. cor</i> | 10. <i>Alasmidonta marginata</i> |
| 3. <i>F. barnesiana tumescens</i> | 11. <i>Obliquaria reflexa</i> |
| 4. <i>Amblema plicata costata</i> | 12. <i>Nephronaias ligamentina gibba</i> |
| 5. <i>Quadrula pustulosa</i> | 13. <i>Plagiola lineolata</i> |
| 6. <i>Plethobasus cooperianus</i> | 14. <i>Eurynia vanuxemensis</i> |
| 7. <i>Pleurobema obliquum rubrum</i> | 15. <i>Lampsilis fasciola</i> |
| 8. <i>Elliptio niger</i> | 16. <i>Truncilla propinqua</i> |

(SMALL TRIBUTARIES OF CLINCH.)

Panther Creek, Hancock Co., Tenn. (near Sneedville, also spelled Painter Creek).

Walker coll.

1. *Strophitus edentulus*

Cove Creek, Caryville, Campbell Co., Tenn.

* = Walker coll.; † = Carn. Mus. (Ortmann, Sept. 12, '15).

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|-------------------------------------|---------------------------------|
| †1. <i>Fusconaia barnesiana</i> | †4. <i>Medionidus plateolus</i> |
| †2. <i>F. barnesiana bigbyensis</i> | †5. <i>Eurynia nebulosa</i> |
| *†3. <i>Lasmigona badia</i> | †6. <i>E. vanuxemensis</i> |

Coal Creek, Anderson Co., Tenn.

* = Walker coll.; ‡ = reported by Call.

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|----------------------------------|--------------------------------|
| *†1. <i>Fusconaia barnesiana</i> | *2. <i>Lampsilis virescens</i> |
|----------------------------------|--------------------------------|

Cane Creek, Offutt, Anderson Co., Tenn.

(Ortmann, Sept. 1, '14).

1. *Eurynia vanuxemensis* (seen)

Bull Run, Heiskell, Knox Co., Tenn.

Walker coll.

1. *Lasmigona badia*

(DRAINAGE OF POPLAR CREEK.)

Brush Fork, Marlow, Anderson Co., Tenn.

Carn. Mus. (Ortmann, Sept. 2, '14).

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|-----------------------------|--------------------------------|
| 1. <i>Alasmidonta minor</i> | 3. <i>Eurynia vanuxemensis</i> |
| 2. <i>Eurynia nebulosa</i> | |

Poplar Creek, Roane Co., Tenn.

* = Walker coll.; ‡ = reported by Call.

- | | |
|------------------------------------|------------------------------------|
| *1. <i>Fusconaia cuneolus</i> } | *4. <i>Amblema plicata costata</i> |
| *†2. <i>F. cuneolus appressa</i> } | *5. <i>Pleurobema oviforme</i> |
| *3. <i>F. cor</i> | |

Emory River, Harriman Junction, Roane Co., Tenn.

Carn. Mus. (Ortmann, May 15, '15).

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|--------------------------|----------------------------|
| 1. <i>Elliptio niger</i> | 2. <i>Eurynia nebulosa</i> |
|--------------------------|----------------------------|

Emory River, Harriman, Roane Co., Tenn.

‡ = according to Pilsbry & Rhoads; † = Carn. Mus. (Ortmann, May 16, '15).

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|------------------------------------|----------------------------------|
| ‡†1. <i>Fusconaia cuneolus</i> | ‡†10. <i>Toxolasma lividum</i> |
| ‡2. <i>F. barnesiana tumescens</i> | ‡11. <i>Medionidus plateolus</i> |
| †3. <i>Amblema plicata costata</i> | †12. <i>Eurynia perpurpurea</i> |
| †4. <i>Pleurobema oviforme</i> | †13. <i>E. nebulosa</i> |
| ‡5. <i>P. oviforme holstonense</i> | ‡14. <i>E. vanuxemensis</i> |
| 6. <i>Elliptio niger</i> (seen) | †15. <i>Lampsilis virescens</i> |
| ‡†7. <i>E. dilatatus</i> | †16. <i>L. ovata ventricosa</i> |
| 8. <i>Lasmigona costata</i> (seen) | ‡17. <i>L. fasciola</i> |
| ‡†9. <i>Ellipsaria fasciolaris</i> | †18. <i>Truncilla turgidula</i> |

HOLSTON DRAINAGE.

(HEADWATERS.)

Little Mocassin Creek, Gate City, Scott Co., Va.

Carn. Mus. (Ortmann, May 16, '13).

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|---------------------------|--------------------------------|
| 1. <i>Lasmigona badia</i> | 2. <i>Eurynia vanuxemensis</i> |
|---------------------------|--------------------------------|

Big Mocassin Creek, Willow Spring, Russell Co., Va.

Walker coll.

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|---|---|
| 1. <i>Fusconaia barnesiana bigbyensis</i> | 2. <i>Pleurobema oviforme argenteum</i> |
|---|---|

Big Mocassin Creek, Mocassin Gap, Scott Co., Va.

Carn. Mus. (Ortmann, May 16, '13; Sept. 9, '15).

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|---|---------------------------------------|
| 1. <i>Fusconaia cuneolus</i> | 9. <i>Ellipsaria subtenta</i> |
| 2. <i>F. barnesiana</i> | 10. <i>Medionidus plateolus</i> |
| 3. <i>F. barnesiana bigbyensis</i> } | 11. <i>Eurynia nebulosa</i> |
| 4. <i>Quadrula cylindrica</i> | 12. <i>E. vanuxemensis</i> |
| 5. <i>Pleurobema oviforme argenteum</i> | 13. <i>Lampsilis ovata ventricosa</i> |
| 6. <i>Alasmidonta minor</i> | 14. <i>L. fasciola</i> |
| 7. <i>A. marginata</i> | 15. <i>Truncilla capsæformis</i> |
| 8. <i>Pegias fabula</i> | |

North Fork Holston River, Saltville, Smyth Co., Va.

† = Carn. Mus. (Ortmann, Sept. 17, '12); * = Carn. Mus. (O. A. Peterson, June 20, '17).

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|---|---|
| †*1. <i>Fusconaia barnesiana bigbyensis</i> | †*3. <i>Pleurobema oviforme argenteum</i> |
| †*2. <i>Lexingtonia dolabelloides conradi</i> | †4. <i>Lasmigona costata</i> |
| | †5. <i>Alasmidonta minor</i> |

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|-----------------------------------|--|
| †6. <i>A. marginata</i> | †*12. <i>Medionidus plateolus</i> |
| †*7. <i>Pegias fabula</i> | †*13. <i>Eurynia nebulosa</i> |
| †8. <i>Strophitus edentulus</i> | †*14. <i>E. vanuxemensis</i> |
| †*9. <i>Ellipsaria subtenta</i> | †15. <i>Lampsilis ovata ventricosa</i> |
| †10. <i>Nephronaias pectorosa</i> | †16. <i>L. fasciola</i> |
| *11. <i>Toxolasma lividum</i> | |

North Fork Holston River, Holston, Washington Co., Va.

Walker coll. (Adams, Aug. 13, '01).

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|--|----------------------------------|
| 1. <i>Fusconaia cor analoga</i> | 8. <i>Pegias fabula</i> |
| 2. <i>F. barnesiana</i> | 9. <i>Ellipsaria subtenta</i> |
| 3. <i>F. barnesiana bigbyensis</i> } | 10. <i>Nephronaias pectorosa</i> |
| 4. <i>Lexingtonia dolabelloides con-</i> | 11. <i>Toxolasma lividum</i> |
| radi | 12. <i>Lemiox rimosus</i> |
| 5. <i>Pleurobema oviforme argenteum</i> | 13. <i>Medionidus plateolus</i> |
| 6. <i>Elliptio dilatatus</i> | 14. <i>Eurynia nebulosa</i> |
| 7. <i>Lasmigona costata</i> | 15. <i>Lampsilis fasciola</i> |

North Fork Holston River, Mendota, Washington Co., Va.

* = Walker coll. (Adams, Oct. 13, '00); † = Carn. Mus. (Ortmann, July 5, '13).

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|---|--|
| †1. <i>Fusconaia pilaris bursa-pastoris</i> | †14. <i>Alasmidonta marginata</i> |
| †2. <i>F. cuneolus</i> | †15. <i>Pegias fabula</i> |
| *†3. <i>F. cor analoga</i> | †16. <i>Ellipsaria fasciolaris</i> |
| †4. <i>F. barnesiana</i> | *†17. <i>E. subtenta</i> |
| †5. <i>F. barnesiana bigbyensis</i> | †18. <i>Nephronaias pectorosa</i> |
| †6. <i>Quadrula intermedia</i> | *19. <i>Medionidus plateolus</i> |
| †7. <i>Q. cylindrica strigillata</i> | †20. <i>Eurynia perpurpurea</i> |
| 8. <i>Rotundaria tuberculata</i> | *†21. <i>E. nebulosa</i> |
| *†9. <i>Lexingtonia dolabelloides con-</i> | †22. <i>E. vanuxemensis</i> |
| radi | †23. <i>Lampsilis ovata ventricosa</i> |
| †10. <i>Pleurobema oviforme</i> } | †24. <i>L. fasciola</i> |
| †11. <i>P. oviforme argenteum</i> } | †25. <i>Truncilla triquetra</i> |
| *†12. <i>Elliptio dilatatus</i> | *26. <i>T. capsaeformis</i> |
| †13. <i>Lasmigona costata</i> | |

North Fork Holston River, Hilton, Scott Co., Va.

Carn. Mus. (Ortmann, July 7, '13).

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|--|--|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> | 7. <i>Rotundaria tuberculata</i> |
| 2. <i>F. pilaris lesueuriana</i> | 8. <i>Lexingtonia dolabelloides con-</i> |
| 3. <i>F. cuneolus</i> | radi |
| 4. <i>F. cor analoga</i> | 9. <i>Pleurobema oviforme</i> } |
| 5. <i>Amblema plicata costata</i> | 10. <i>P. oviforme argenteum</i> } |
| 6. <i>Quadrula cylindrica strigillata</i> | 11. <i>Elliptio dilatatus</i> |

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|-----------------------------------|---------------------------------------|
| 12. <i>Lasmigona costata</i> | 21. <i>E. nebulosa</i> |
| 13. <i>Alasmidonta marginata</i> | 22. <i>E. vanuxemensis</i> |
| 14. <i>Strophitus edentulus</i> | 23. <i>Lampsilis ovata ventricosa</i> |
| 15. <i>Ellipsaria fasciolaris</i> | 24. <i>L. fasciola</i> |
| 16. <i>Nephronaias pectorosa</i> | 25. <i>Truncilla triquetra</i> |
| 17. <i>Lemiox rimosus</i> | 26. <i>T. interrupta</i> |
| 18. <i>Medionidus plateolus</i> | 27. <i>T. haysiana</i> |
| 19. <i>Eurynia fabalis</i> | 28. <i>T. capsæformis</i> |
| 20. <i>E. perpurpurea</i> | |

North Fork Holston River, Holston Bridge, Scott Co., Va.

Walker coll. (Adams, Aug. 11, '01).

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|---|-------------------------------------|
| 1. <i>Fusconaia pilaris lesueuriana</i> | 9. <i>Nephronaias pectorosa</i> |
| 2. <i>F. cor analoga</i> | 10. <i>Toxolasma lividum</i> |
| 3. <i>F. barnesiana bigbyensis</i> | 11. <i>Eurynia vanuxemensis</i> |
| 4. <i>Quadrula cylindrica strigillata</i> | 12. <i>Lampsilis fasciola</i> |
| 5. <i>Elliptio dilatatus</i> | 13. <i>Truncilla triquetra</i> |
| 6. <i>Lasmigona costata</i> | 14. <i>T. interrupta</i> |
| 7. <i>Ellipsaria subtenta</i> | 15. <i>T. torulosa gubernaculum</i> |
| 8. <i>Nephronaias ligamentina gibba</i> | 16. <i>T. capsæformis</i> |

North Fork Holston River, Rotherwood, Hawkins Co., Tenn.

Carn. Mus. (Ortmann, July 13, '13; Sept. 5, '13).

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|--|--|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> } | 19. <i>Ellipsaria subtenta</i> |
| 2. <i>F. pilaris lesueuriana</i> } | 20. <i>Nephronaias ligamentina gibba</i> |
| 3. <i>F. cuneolus</i> | 21. <i>N. pectorosa</i> |
| 4. <i>F. cor analoga</i> | 22. <i>Proptera alata</i> (seen) |
| 5. <i>F. barnesiana</i> } | 23. <i>Lemiox rimosus</i> |
| 6. <i>F. barnesiana bigbyensis</i> } | 24. <i>Medionidus plateolus</i> |
| 7. <i>Amblesma plicata costata</i> | 25. <i>Eurynia fabalis</i> |
| 8. <i>Quadrula cylindrica strigillata</i> | 26. <i>E. perpurpurea</i> |
| 9. <i>Rotundaria tuberculata</i> | 27. <i>E. nebulosa</i> |
| 10. <i>Plethobasus cyphus</i> | 28. <i>E. vanuxemensis</i> |
| 11. <i>Lexingtonia dolabelloides conradi</i> | 29. <i>E. recta</i> |
| 12. <i>Pleurobema oviforme</i> } | 30. <i>Lampsilis ovata ventricosa</i> |
| 13. <i>P. oviforme argenteum</i> } | 31. <i>L. fasciola</i> |
| 14. <i>Elliptio dilatatus</i> | 32. <i>Truncilla triquetra</i> |
| 15. <i>Lasmigona costata</i> | 33. <i>T. interrupta</i> |
| 16. <i>Alasmidonta marginata</i> | 34. <i>T. lenior</i> |
| 17. <i>Strophitus edentulus</i> | 35. <i>T. haysiana</i> |
| 18. <i>Ellipsaria fasciolaris</i> | 36. <i>T. torulosa gubernaculum</i> |
| | 37. <i>T. capsæformis</i> |

Middle Fork Holston River, Marion, Smyth Co., Va.

Carn. Mus. (Ortmann, Sept. 16, '12).

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|----------------------------|--------------------------------|
| 1. <i>Eurynia nebulosa</i> | 2. <i>Eurynia vanuxemensis</i> |
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Middle Fork Holston River, Chilhowie, Smyth Co., Va.

Carn. Mus. (Ortmann, May 20, '13).

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|---|--------------------------------|
| 1. <i>Fusconaia barnesiana bigbyensis</i> | 7. <i>Ellipsaria subtenta</i> |
| 2. <i>Pleurobema oviforme argenteum</i> | 8. <i>Medionidus plateolus</i> |
| 3. <i>Elliptio dilatatus</i> | 9. <i>Eurynia nebulosa</i> |
| 4. <i>Lasmigona costata</i> | 10. <i>E. vanuxemensis</i> |
| 5. <i>Alasmidonta minor</i> | 11. <i>Lampsilis fasciola</i> |
| 6. <i>A. marginata</i> | 12. <i>Truncilla walkeri</i> |

Laurel Creek, Mock's Mill (near Vestal P. O.), Washington Co., Va.

Walker coll. (Adams, Aug. 26, '01).

1. *Fusconaia barnesiana bigbyensis*

South Fork Holston River, Barron, Washington Co., Va.

* = Walker coll. (Adams, Aug. 14, '01); † = Carn. Mus. (Ortmann, May 19, '13).

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|--|----------------------------------|
| †1. <i>Fusconaia barnesiana bigbyensis</i> | *8. <i>Nephronaias pectorosa</i> |
| †2. <i>Pleurobema oviforme argenteum</i> | *†9. <i>Medionidus plateolus</i> |
| *3. <i>Elliptio dilatatus</i> | *†10. <i>Eurynia nebulosa</i> |
| *4. <i>Lasmigona costata</i> | *†11. <i>E. vanuxemensis</i> |
| †5. <i>Alasmidonta minor</i> | *†12. <i>Lampsilis fasciola</i> |
| *6. <i>A. marginata</i> | *†13. <i>Truncilla walkeri</i> |
| *7. <i>Ellipsaria subtenta</i> | |

South Fork Holston River, Fish Dam, Sullivan Co., Tenn.

Walker coll. (Adams, Sept. 6, '01).

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|---|------------------------------|
| 1. <i>Lexingtonia dolabelloides conradi</i> | 4. <i>Eurynia nebulosa</i> |
| 2. <i>Elliptio dilatatus</i> | 5. <i>E. vanuxemensis</i> |
| 3. <i>Nephronaias pectorosa</i> | 6. <i>Lampsilis fasciola</i> |

South Fork Holston River, Emmett, Sullivan Co., Tenn.

Carn. Mus. (Ortmann, July 9, '13).

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|---|---------------------------------------|
| 1. <i>Fusconaia barnesiana bigbyensis</i> | 8. <i>Ellipsaria fasciolaris</i> |
| 2. <i>Lexingtonia dolabelloides conradi</i> | 9. <i>Ellipsaria subtenta</i> |
| 3. <i>Pleurobema oviforme</i> } | 10. <i>Nephronaias pectorosa</i> |
| 4. <i>P. oviforme argenteum</i> } | 11. <i>Eurynia nebulosa</i> |
| 5. <i>Elliptio dilatatus</i> | 12. <i>E. vanuxemensis</i> |
| 5. <i>Lasmigona costata</i> | 13. <i>Lampsilis ovata ventricosa</i> |
| 7. <i>Alasmidonta marginata</i> | 14. <i>L. fasciola</i> |
| | 15. <i>Truncilla walkeri</i> |

South Fork Holston, Bluff City, Sullivan Co., Tenn.

Carn. Mus. (Ortmann, July 10, '13).

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|--|---------------------------------------|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> } | 10. <i>Lasmigona costata</i> |
| 2. <i>F. pilaris lesueuriana</i> } | 11. <i>Alasmidonta marginata</i> |
| 3. <i>F. barnesiana</i> } | 12. <i>Strophitus edentulus</i> |
| 4. <i>F. barnesiana bigbyensis</i> } | 13. <i>Ellipsaria fasciolaris</i> |
| 5. <i>Quadrula intermedia</i> | 14. <i>E. subtenta</i> (seen) |
| 6. <i>Lexingtonia dolabelloides conradi</i> | 15. <i>Nephronaias pectorosa</i> |
| 7. <i>Pleurobema oviforme argenteum</i> | 16. <i>Eurynia nebulosa</i> |
| 8. <i>Elliptio dilatatus</i> | 17. <i>E. vanuxemensis</i> |
| 9. <i>Lasmigona badia</i> | 18. <i>Lampsilis ovata ventricosa</i> |
| | 19. <i>L. fasciola</i> |

Beaver Creek, Bristol, Washington Co., Va.

Carn. Mus. (Ortmann, July 6, '13).

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|-----------------------------|--------------------------------|
| 1. <i>Alasmidonta minor</i> | 2. <i>Medionidus plateolus</i> |
|-----------------------------|--------------------------------|

South Fork Holston River, Pactolus, Sullivan Co., Tenn.

Carn. Mus. (Ortmann, May 20, '14).

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|--|--|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> } | 15. <i>Strophitus edentulus</i> |
| 2. <i>F. pilaris lesueuriana</i> } | 16. <i>Ellipsaria fasciolaris</i> |
| 3. <i>F. barnesiana</i> | 17. <i>E. subtenta</i> |
| 4. <i>Amblema plicata costata</i> | 18. <i>Nephronaias ligamentina gibba</i> |
| 5. <i>Quadrula intermedia</i> | 19. <i>N. pectorosa</i> |
| 6. <i>Q. cylindrica strigillata</i> | 20. <i>Medionidus plateolus</i> |
| 7. <i>Rotundaria tuberculata</i> | 21. <i>Eurynia fabalis</i> |
| 8. <i>Pleurobema oviforme</i> | 22. <i>Lampsilis ovata ventricosa</i> |
| 9. <i>P. oviforme argenteum</i> | 23. <i>L. fasciola</i> |
| 10. <i>Elliptio niger</i> | 24. <i>Truncilla triquetra</i> |
| 11. <i>E. dilatatus</i> | 25. <i>T. lenior</i> |
| 12. <i>Lasmigona costata</i> | 26. <i>T. haysiana</i> |
| 13. <i>Alasmidonta marginata</i> | 27. <i>T. torulosa gubernaculum</i> |
| 14. <i>Pegias fabula</i> | 28. <i>T. capsæformis</i> |

Watauga River, Watauga, Carter Co., Tenn.

‡=according to Pilsbry & Rhoads; †=Carn. Mus. (Ortmann, July 14, '13).

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|---|----------------------------------|
| †1. <i>Fusconaia pilaris bursa-pastoris</i> | ‡5. <i>Nephronaias pectorosa</i> |
| ††2. <i>F. barnesiana bigbyensis</i> | †6. <i>Eurynia nebulosa</i> |
| †3. <i>Pleurobema oviforme argenteum</i> | †7. <i>E. vanuxemensis</i> |
| †4. <i>Lasmigona badia</i> | †8. <i>Lampsilis fasciola</i> |

Watauga River, Johnson City, Washington Co., Tenn.

According to Pilsbry & Rhoads.

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|--|--------------------------------|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> | 6. <i>Medionidus plateolus</i> |
| 2. <i>Elliptio dilatatus</i> | 7. <i>Eurynia nebulosa</i> |
| 3. <i>Lasmigona costata</i> | 8. <i>E. vanuxemensis</i> |
| 4. <i>Alasmidonta marginata</i> | 9. <i>Lampsilis fasciola</i> |
| 5. <i>Strophitus edentulus</i> | |

(HOLSTON PROPER.)

Holston River, Church Hill, Hawkins Co., Tenn.

Carn. Mus. (Ortmann, Aug. 25, '14).

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|--|--|
| 1. <i>Fusconaia pilaris bursa-pastoris</i> | 9. <i>Lasmigona badia</i> |
| 2. <i>F. pilaris lesueuriana</i> | 10. <i>L. costata</i> |
| 3. <i>Amblema plicata costata</i> (seen) | 11. <i>Nephronaias ligamentina gibba</i> |
| 4. <i>Quadrula intermedia</i> (seen) | 12. <i>Proptera alata</i> (seen) |
| 5. <i>Q. cylindrica</i> | 13. <i>Eurynia fabalis</i> |
| 6. <i>Rotundaria tuberculata</i> | 14. <i>Truncilla lenior</i> |
| 7. <i>Elliptio niger</i> (seen) | 15. <i>T. haysiana</i> |
| 8. <i>E. dilatatus</i> | 16. <i>T. capsæformis</i> |

Holston River, Austin Mill, Hawkins Co., Tenn.

* = Walker coll. ("Rogersville," practically the same locality);

† = Carn. Mus. (Ortmann, Aug. 24, '14).

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|---|---|
| 1. <i>Cumberlandia monodonta</i> (seen) | †14. <i>Ellipsaria fasciolaris</i> |
| 2. <i>Fusconaia pilaris lesueuriana</i>
(seen) | †15. <i>Nephronaias ligamentina gibba</i> |
| †3. <i>F. cuneolus</i> | †16. <i>N. pectorosa</i> |
| †4. <i>F. cuneolus appressa</i> | *17. <i>Toxolasma lividum</i> |
| †5. <i>F. barnesiana</i> | *18. <i>Lemiox rimosus</i> |
| †6. <i>Amblema plicata costata</i> | †19. <i>Eurynia nebulosa</i> |
| †7. <i>Quadrula cylindrica</i> | †20. <i>Lampsilis ovata ventricosa</i> |
| †8. <i>Rotundaria tuberculata</i> | †21. <i>Truncilla triquetra</i> |
| †9. <i>Pleurobema obliquum rubrum</i> | †22. <i>T. arcæformis</i> |
| †10. <i>Elliptio niger</i> | *†23. <i>T. haysiana</i> |
| †11. <i>E. dilatatus</i> | *24. <i>T. torulosa gubernaculum</i> |
| †12. <i>Lasmigona costata</i> | *†25. <i>T. turgidula</i> |
| †13. <i>Alasmidonta marginata</i> | *†26. <i>T. capsæformis</i> |

Holston River, Holston Station, Grainger Co., Tenn.

* = Walker coll. (Adams); † = Carn. Mus. (Ortmann, Sept. 15, '13).

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|---|------------------------------------|
| †1. <i>Fusconaia pilaris lesueuriana</i> | *†20. <i>Nephronaias pectorosa</i> |
| †2. <i>F. cuneolus</i> | †21. <i>Paraptera leptodon</i> |
| †3. <i>F. barnesiana</i> | †22. <i>P. fragilis</i> |
| *4. <i>Rotundaria tuberculata</i> (seen) | †23. <i>Proptera alata</i> |
| †5. <i>Pleurobatus cyphus</i> | †24. <i>Medionidus plateolus</i> |
| †6. <i>Pleurobema obliquum</i> | †25. <i>Eurynia recta</i> |
| †7. <i>P. obliquum cordatum</i> | †26. <i>Lampsilis ovata</i> |
| †8. <i>P. obliquum rubrum</i> | †27. <i>L. ovata ventricosa</i> |
| †9. <i>P. oviforme</i> | †28. <i>L. fasciola</i> |
| *10. <i>Elliptio niger</i> | †29. <i>Truncilla triquetra</i> |
| †11. <i>E. dilatatus</i> | †30. <i>T. arcaformis</i> |
| †12. <i>Lasmigona costata</i> | †31. <i>T. interrupta</i> |
| †13. <i>Alasmidonta marginata</i> | †32. <i>T. haysiana</i> |
| †14. <i>Strophitus edentulus</i> | †33. <i>T. stewardsoni</i> |
| †15. <i>Ellipsaria fasciolaris</i> | †34. <i>T. lewisi</i> |
| †16. <i>E. subtenta</i> | †35. <i>T. turgidula</i> |
| *†17. <i>Dromus dromas caperatus</i> | †36. <i>T. florentina</i> |
| †18. <i>Obovaria subrotunda levigata</i> | †37. <i>T. capsaeformis</i> |
| †19. <i>Nephronaias ligamentina gibba</i> | |

Holston River, Noeton, Grainger Co., Tenn.

Carn. Mus. (Ortmann, May 22, '14).

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|-----------------------------------|--|
| 1. <i>Cumberlandia monodonta</i> | 18. <i>Lasmigona costata</i> |
| 2. <i>Fusconaia pilaris</i> | 19. <i>Strophitus edentulus</i> |
| 3. <i>F. pilaris lesueuriana</i> | 20. <i>Ellipsaria fasciolaris</i> |
| 4. <i>F. cuneolus</i> | 21. <i>E. subtenta</i> |
| 5. <i>F. cuneolus appressa</i> | 22. <i>Dromus dromas caperatus</i> |
| 6. <i>F. barnesiana</i> | 23. <i>Nephronaias ligamentina gibba</i> |
| 7. <i>F. barnesiana tumescens</i> | 24. <i>Paraptera leptodon</i> |
| 8. <i>Amblema plicata costata</i> | 25. <i>P. fragilis</i> |
| 9. <i>Quadrula cylindrica</i> | 26. <i>Proptera alata</i> |
| 10. <i>Rotundaria tuberculata</i> | 27. <i>Eurynia fabalis</i> |
| 11. <i>Pleurobema obliquum</i> | 28. <i>E. nebulosa</i> |
| 12. <i>P. obliquum catillus</i> | 29. <i>E. recta</i> |
| 13. <i>P. obliquum coccineum</i> | 30. <i>Lampsilis ovata ventricosa</i> |
| 14. <i>P. obliquum rubrum</i> | 31. <i>Truncilla arcaformis</i> |
| 15. <i>P. oviforme</i> | 32. <i>T. haysiana</i> |
| 16. <i>Elliptio niger</i> | 33. <i>T. turgidula</i> |
| 17. <i>E. dilatatus</i> | 34. <i>T. capsaeformis</i> |

Holston River, Turley Mill, Grainger Co., Tenn.

Carn. Mus. (Ortmann, May 23, '14).

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|--------------------------------------|--|
| 1. <i>Fusconaia pilaris</i> | 19. <i>Nephronaias ligamentina gibba</i> |
| 2. <i>F. pilaris lesueuriana</i> | 20. <i>N. pectorosa</i> |
| 3. <i>F. pilaris bursa-pastoris</i> | 21. <i>Paraptera fragilis</i> |
| 4. <i>F. cuneolus</i> | 22. <i>Proptera alata</i> |
| 5. <i>F. barnesiana tumescens</i> | 23. <i>Lemiox rimosus</i> |
| 6. <i>Amblema plicata costata</i> | 24. <i>Eurynia nebulosa</i> |
| 7. <i>Quadrula cylindrica</i> | 25. <i>E. recta</i> |
| 8. <i>Rotundaria tuberculata</i> | 26. <i>Lampsilis ovata</i> |
| 9. <i>Pleurobema obliquum rubrum</i> | 27. <i>L. ovata ventricosa</i> |
| 10. <i>P. oviforme</i> | 28. <i>L. fasciola</i> |
| 11. <i>Elliptio niger</i> (seen) | 29. <i>Truncilla triquetra</i> |
| 12. <i>E. dilatatus</i> | 30. <i>T. arcæformis</i> |
| 13. <i>Lasmigona costata</i> | 31. <i>T. interrupta</i> |
| 14. <i>Alasmidonta marginata</i> | 32. <i>T. haysiana</i> |
| 15. <i>Strophitus edentulus</i> | 33. <i>T. turgidula</i> |
| 16. <i>Ellipsaria fasciolaris</i> | 34. <i>T. florentina</i> |
| 17. <i>Cyprogenia stegaria</i> | 35. <i>T. capsæformis</i> |
| 18. <i>Dromus dromas caperatus</i> | |

Holston River, McBee Ford, Hodges, Jefferson Co., Tenn.

Carn. Mus. (Ortmann, May 25, '14).

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|---|--|
| 1. <i>Cumberlandia monodonta</i> (seen) | 19. <i>Strophitus edentulus</i> |
| 2. <i>Fusconaia pilaris lesueuriana</i> | 20. <i>Ellipsaria fasciolaris</i> (seen) |
| 3. <i>F. barnesiana</i> | 21. <i>E. subienta</i> (seen) |
| 4. <i>F. barnesiana tumescens</i> | 22. <i>Cyprogenia stegaria</i> |
| 5. <i>Amblema plicata costata</i> | 23. <i>Dromus dromas caperatus</i> |
| 6. <i>Quadrula pustulosa</i> | 24. <i>Nephronaias ligamentina gibba</i> |
| 7. <i>Q. cylindrica</i> | 25. <i>Amygdaloniaia truncata</i> |
| 8. <i>Rotundaria tuberculata</i> | 26. <i>Paraptera fragilis</i> |
| 9. <i>Plethobasus cyphyus</i> | 27. <i>Proptera alata</i> |
| 10. <i>Pleurobema obliquum</i> | 28. <i>Eurynia recta</i> |
| 11. <i>P. obliquum cordatum</i> | 29. <i>Lampsilis ovata</i> |
| 12. <i>P. obliquum coccineum</i> | 30. <i>L. ovata ventricosa</i> } |
| 13. <i>P. obliquum rubrum</i> | 31. <i>Truncilla arcæformis</i> |
| 14. <i>P. oviforme</i> | 32. <i>T. interrupta</i> |
| 15. <i>Elliptio niger</i> | 33. <i>T. haysiana</i> |
| 16. <i>E. dilatatus</i> | 34. <i>T. torulosa gubernaculum</i> |
| 17. <i>Lasmigona costata</i> | 35. <i>T. turgidula</i> |
| 18. <i>Alasmidonta marginata</i> | 36. <i>T. capsæformis</i> |

Holston River, Gant Island, near Strawberry Plains, Jefferson Co., Tenn.

Walker coll. (Adams, Sept. 29, '00).

1. *Truncilla arcæformis*

Holston River, Mascot, Knox Co., Tenn.

Carn. Mus. (Ortmann, Sept. 6, '14; Sept. 16, '15).

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|--|--|
| 1. <i>Cumberlandia monodonta</i> | 24. <i>Dromus dromas caperatus</i> |
| 2. <i>Fusconaia pilaris</i> } | 25. <i>Obovaria surotunda</i> } |
| 3. <i>F. pilaris lesueuriana</i> } | 26. <i>O. subrotunda levigata</i> } |
| 4. <i>F. barnesiana</i> | 27. <i>Nephronaias ligamentina gibba</i> |
| 5. <i>Amblema plicata costata</i> (seen) | 28. <i>N. pectorosa</i> (seen) |
| 6. <i>Quadrula pustulosa</i> | 29. <i>Paraptera fragilis</i> |
| 7. <i>Q. metanevra</i> | 30. <i>Proptera alata</i> |
| 8. <i>Q. cylindrica</i> | 31. <i>Lemiox rimosus</i> |
| 9. <i>Rotundaria tuberculata</i> | 32. <i>Medionidus plateolus</i> |
| 10. <i>Plethobasus cyphus</i> | 33. <i>Eurynia fabalis</i> |
| 11. <i>Pleurobema obliquum</i> } | 34. <i>E. recta</i> |
| 12. <i>P. obliquum cordatum</i> } | 35. <i>Lampsilis ovata</i> } |
| 13. <i>P. obliquum rubrum</i> } | 36. <i>L. ovata ventricosa</i> } |
| 14. <i>P. oviforme</i> | 37. <i>L. fasciola</i> |
| 15. <i>P. oviforme holstonense</i> | 38. <i>Truncilla triquetra</i> |
| 16. <i>Elliptio niger</i> | 39. <i>T. arcaformis</i> |
| 17. <i>E. dilatatus</i> | 40. <i>T. interrupta</i> |
| 18. <i>Lasmigona costata</i> | 41. <i>T. haysiana</i> |
| 19. <i>Alasmidonta marginata</i> | 42. <i>T. stewardsoni</i> |
| 20. <i>Strophitus edentulus</i> | 43. <i>T. torulosa gubernaculum</i> |
| 21. <i>Ellipsaria fasciolaris</i> | 44. <i>T. turgidula</i> |
| 22. <i>E. subtenta</i> | 45. <i>T. florentina</i> |
| 23. <i>Cyprogenia stegaria</i> | 46. <i>T. capsæformis</i> |

Holston River, McMillan, Knox Co., Tenn.

Carn. Mus. (Ortmann, Sept. 16, '13).

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|--|--------------------------------|
| 1. <i>Cumberlandia monodonta</i> | 14. <i>Proptera alata</i> |
| 2. <i>Fusconaia pilaris lesueuriana</i> | 15. <i>Eurynia nebulosa</i> |
| 3. <i>Quadrula pustulosa</i> | 16. <i>E. recta</i> |
| 4. <i>Q. cylindrica</i> | 17. <i>Lampsilis ovata</i> |
| 5. <i>Rotundaria tuberculata</i> | 18. <i>L. ovata ventricosa</i> |
| 6. <i>Plethobasus cyphus</i> | 19. <i>L. fasciola</i> |
| 7. <i>Pleurobema obliquum rubrum</i> | 20. <i>Truncilla triquetra</i> |
| 8. <i>Elliptio niger</i> | 21. <i>T. arcaformis</i> |
| 9. <i>E. dilatatus</i> | 22. <i>T. interrupta</i> |
| 10. <i>Strophitus edentulus</i> | 23. <i>T. stewardsoni</i> |
| 11. <i>Dromus dromas caperatus</i> | 24. <i>T. florentina</i> |
| 12. <i>Nephronaias ligamentina gibba</i> | 25. <i>T. capsæformis</i> |
| 13. <i>N. pectorosa</i> | |

Holston River, Boyd Island, Knoxville, Knox Co., Tenn.

According to Pilsbry & Rhoads ("1 mile above junction with French Broad").

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|-----------------------------------|--|
| 1. <i>Fusconaia pilaris</i> | 10. <i>Cyprogenia stegaria</i> |
| 2. <i>Quadrula pustulosa</i> | 11. <i>Dromus dromas</i> |
| 3. <i>Q. cylindrica</i> | 12. <i>Nephronaias ligamentina gibba</i> |
| 4. <i>Rotundaria tuberculata</i> | 13. <i>Paraptera fragilis</i> |
| 5. <i>Pleurobema obliquum</i> | 14. <i>Eurynia recta</i> |
| 6. <i>P. obliquum rubrum</i> | 15. <i>Lampsilis ovata</i> |
| 7. <i>P. oviforme holstonense</i> | 16. <i>Truncilla arcæformis</i> |
| 8. <i>Elliptio niger</i> | 17. <i>T. propinqua</i> |
| 9. <i>E. dilatatus</i> | |

(SMALL TRIBUTARIES OF HOLSTON PROPER.)

Big Creek, Rogersville, Hawkins Co., Tenn.

Walker coll.

- | | |
|----------------------------|--------------------------------|
| 1. <i>Lasmigona badia</i> | 3. <i>Medionidus plateolus</i> |
| 2. <i>Alamidonta minor</i> | |

Big Flat Creek, Corryton, Knox Co., Tenn.

Carn. Mus. (Ortmann, May 12, '14).

- | | |
|--------------------------------|----------------------------------|
| 1. <i>Fusconaia barnesiana</i> | 3. <i>Eurynia nebulosa</i> |
| 2. <i>Lasmigona badia</i> | 4. <i>E. vanuxemensis</i> (seen) |

NOLICHUCKY RIVER DRAINAGE.

Whitehorn Creek, Bulls Gap, Hawkins Co., Tenn.

Carn. Mus. (Ortmann, May 18, '14).

- | | |
|----------------------------|--------------------------------|
| 1. <i>Lasmigona badia</i> | 3. <i>Eurynia vanuxemensis</i> |
| 2. <i>Eurynia nebulosa</i> | |

Bent Creek, Whitesburg, Hamblen Co., Tenn.

Carn. Mus. (Ortmann, Sept. 8, '15).

- | | |
|-----------------------------------|--------------------------------|
| 1. <i>Lasmigona badia</i> | 3. <i>Eurynia vanuxemensis</i> |
| 2. <i>Eurynia nebulosa</i> (seen) | |

Nolichucky River, Chunn's Shoals, Hamblen Co., Tenn.

Carn. Mus. (Ortmann, Sept. 17, '13) (within a mile from confluence with French Broad).

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|---|---------------------------------------|
| 1. <i>Fusconaia cuneolus appressa</i> | 8. <i>Paraptera fragilis</i> |
| 2. <i>Amblema plicata costata</i> | 9. <i>Proptera alata</i> |
| 3. <i>Quadrula pustulosa</i> | 10. <i>Eurynia recta</i> |
| 4. <i>Rotundaria tuberculata</i> | 11. <i>Lampsilis ovata ventricosa</i> |
| 5. <i>Elliptio niger</i> | 12. <i>Truncilla triquetra</i> |
| 6. <i>Nephronaias ligamentina gibba</i> | 13. <i>T. torulosa gubernaculum</i> |
| 7. <i>N. pectorosa</i> | 14. <i>T. capsæformis</i> |

FRENCH BROAD RIVER DRAINAGE.

French Broad River, Asheville, Buncombe Co., N. Car.

* = Walker coll. (Mrs. Andrews); ‡ = reported by Call.

The French Broad at Asheville is now polluted by lumber industries on Davidson River; repeated attempts on my part (May 13, '14, Sept. 14, '14, May 10, '15) failed to reveal any signs of the presence of shells.

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|---|-----------------------------------|
| *1. <i>Pleurobema oviforme</i> (raveneliana) (also Lea) | ‡4. <i>Ellipsaria fasciolaris</i> |
| *2. <i>Elliptio dilatatus</i> | *‡5. <i>Medionidus plateolus</i> |
| *3. <i>Alasmidonta raveneliana</i> (also Lea) | *‡6. <i>Eurynia nebulosa</i> |
| | *‡7. <i>Lampsilis fasciola</i> |
| | ‡8. <i>Truncilla capsæformis</i> |

Call also gives: *Fusconaia pilaris* and *F. pilaris lesueuriana*, but I have seen no specimens of these from this locality, and these records appear to me as very doubtful.

French Broad River, Hot Springs, Madison Co., N. Car.

According to Conrad, from "Warm Springs."

1. *Toxolasma lividum*

French Broad River, Boyd Creek, Sevier Co., Tenn.

Carn. Mus. (Ortmann, Sept. 10, '14).

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|-------------------------------------|---------------------------------------|
| 1. <i>Fusconaia pilaris</i> } | 8. <i>Plethobasus cooperianus</i> |
| 2. <i>F. pilaris lesueuriana</i> } | 9. <i>P. cyphyus</i> |
| 3. <i>F. barnesiana</i> } | 10. <i>P. cyphyus compertus</i> |
| 4. <i>F. barnesiana tumescens</i> } | 11. <i>Lexingtonia dolabelloides</i> |
| 5. <i>Amblema plicata costata</i> | 12. <i>Pleurobema obliquum</i> } |
| 6. <i>Quadrula pustulosa</i> | 13. <i>P. obliquum cordatum</i> } |
| 7. <i>Rotundaria tuberculata</i> | 14. <i>Pleurobema obliquum rubrum</i> |

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|------------------------------------|---|--|
| 15. <i>P. oviforme</i> | } | 20. <i>Ellipsaria fasciolaris</i> |
| 16. <i>P. oviforme holstonense</i> | | 21. <i>Nephronaias ligamentina gibba</i> |
| 17. <i>Elliptio niger</i> | | 22. <i>Proptera alata</i> |
| 18. <i>E. dilatatus</i> | | 23. <i>Eurynia recta</i> |
| 19. <i>Strophitus edentulus</i> | | 24. <i>Truncilla arcæformis</i> |

(TRIBUTARIES OF FRENCH BROAD.)

Long Creek, near Bridgeport, Cocke Co., Tenn.

* = Walker coll. ; ‡ = reported by Lea.

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|----------------------------|---------------------------------|
| *1. <i>Lasmigona badia</i> | ‡2. <i>Eurynia vanuxemensis</i> |
|----------------------------|---------------------------------|

Big Pigeon River, Canton, Haywood Co., N. Car.

Carn. Mus. (Ortmann, May 14, '14).

- | | |
|-----------------------------------|------------------------------|
| 1. <i>Alasmidonta raveneliana</i> | 2. <i>Lampsilis fasciola</i> |
|-----------------------------------|------------------------------|

Little Pigeon River, Sevierville, Sevier Co., Tenn.

Carn. Mus. (Ortmann, Aug. 31, '14).

- | | | |
|------------------------------------|---|---------------------------------------|
| 1. <i>Fusconaia barnesiana</i> | } | 8. <i>Toxolasma lividum</i> |
| 2. <i>F. barnesiana bigbyensis</i> | | 9. <i>Eurynia nebulosa</i> |
| 3. <i>Pleurobema oviforme</i> | } | 10. <i>E. vanuxemensis</i> |
| 4. <i>P. oviforme argenteum</i> | | 11. <i>Lampsilis ovata ventricosa</i> |
| 5. <i>Elliptio dilatatus</i> | | 12. <i>L. fasciola</i> |
| 6. <i>Lasmigona badia</i> | | 13. <i>Truncilla capsæformis</i> |
| 7. <i>Alasmidonta minor</i> | | |

Boyd Creek, Boyd Creek, Sevier Co., Tenn.

Carn. Mus. (Ortmann, Sept. 5, '14).

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|-----------------------------------|--------------------------------|
| 1. <i>Fusconaia barnesiana</i> | 5. <i>Lasmigona costata</i> |
| 2. <i>Amblema plicata costata</i> | 6. <i>Alasmidonta minor</i> |
| 3. <i>Rotundaria tuberculata</i> | 7. <i>Eurynia vanuxemensis</i> |
| 4. <i>Elliptio dilatatus</i> | |

Pond, draining to French Broad, eight miles above Knoxville, Knox Co., Tenn.

Walker coll. (M. D. Barber).

1. *Anodonta grandis gigantea*

TRIBUTARIES OF TENNESSEE, BELOW KNOXVILLE.

(FROM THE WEST.)

First Creek, Knoxville, Knox Co., Tenn.

Walker coll.

1. *Lasmigona badia*

Second Creek, Knoxville, Knox Co., Tenn.

According to Lea.

1. *Fusconaia barnesiana bigbyensis*

Third Creek, Knoxville, Knox Co., Tenn.

Walker coll.

1. *Lasmigona badia*

Piney River, Spring City, Rhea Co., Tenn.

Carn. Mus. (Ortmann, May 18, '15).

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|---|--|
| <ol style="list-style-type: none"> 1. <i>Lasmigona badia</i> | <ol style="list-style-type: none"> 2. <i>Eurynia vanuxemensis</i> |
|---|--|

Martin Branch of Sale Creek, Rhea Co., Tenn.

Walker coll. (W. A. Marsh). (There is no "Martin Branch" on map; Sale Creek flows from near Dayton, Rhea Co., south into Hamilton Co., and to the Tennessee.)

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|--|---|
| <ol style="list-style-type: none"> 1. <i>Fusconaia barnesiana</i> 2. <i>F. barnesiana bigbyensis</i> | } |
|--|---|

(FROM THE EAST, COMING FROM THE MOUNTAINS.)

*Little River Drainage.**Little River, Walland, Blount Co., Tenn.*

Carn. Mus. (Ortmann, May 12, '15).

- | | |
|--|---|
| <ol style="list-style-type: none"> 1. <i>Fusconaia barnesiana bigbyensis</i> 2. <i>Pleurobema oviforme argenteum</i> 3. <i>Medionidus plateolus</i> | <ol style="list-style-type: none"> 4. <i>Eurynia nebulosa</i> 5. <i>E. vanuxemensis</i> |
|--|---|

Little River, Melrose, Blount Co., Tenn.

Carn. Mus. (Ortmann, Sept. 11, '15).

- | | |
|---|--------------------------------------|
| 1. <i>Fusconaia barnesiana bigbyensis</i> | 6. <i>Eurynia nebulosa</i> |
| 2. <i>Pleurobema oviforme argenteum</i> | 7. <i>E. vanuxemensis</i> |
| 3. <i>Alasmidonta minor</i> | 8. <i>Lampsilis ovata ventricosa</i> |
| 4. <i>Nephronaias pectorosa</i> | 9. <i>L. fasciola</i> |
| 5. <i>Medionidus plateolus</i> | |

Little River, Rockford, Blount Co., Tenn.

Carn. Mus. (Ortmann, Sept. 4, '14).

1. *Eurynia nebulosa*

Little River, Knox Co., Tenn. (lower part).

* = Walker coll.; † = Carn. Mus. (Smith coll.).

- | | |
|------------------------------------|--------------------------------|
| *1. <i>Cumberlandia monodonta</i> | *3. <i>Truncilla triquetra</i> |
| †2. <i>Amblema plicata costata</i> | |

Pistol Creek, Rockford, Blount Co., Tenn.

Carn. Mus. (Ortmann, Sept. 4, '14).

- | | |
|---------------------------------------|-----------------------------|
| 1. <i>Fusconaia cuneolus appressa</i> | 4. <i>Toxolasma lividum</i> |
| 2. <i>F. barnesiana</i> | 5. <i>Eurynia nebulosa</i> |
| 3. <i>Alasmidonta minor</i> | |

LITTLE TENNESSEE RIVER DRAINAGE.

Abram Creek, Blount Co., Tenn.

Walker coll.

1. *Fusconaia barnesiana bigbyensis*

Tellico River, Monroe Co., Tenn.

Walker coll., also reported by Lea.

- | | |
|------------------------------------|---|
| 1. <i>Fusconaia barnesiana</i> | } |
| 2. <i>F. barnesiana bigbyensis</i> | |

Little Tennessee River, Monroe Co., Tenn.

* = Walker coll.; ‡ = according to Marsh.

- | | |
|------------------------------------|-------------------------------|
| ‡1. <i>Fusconaia pilaris</i> | *5. <i>Elliptio dilatatus</i> |
| *2. <i>F. barnesiana tumescens</i> | *6. <i>Lampsilis fasciola</i> |
| *3. <i>Pleurobema oviforme</i> | } |
| *4. <i>P. oviforme holstonense</i> | |

Little Tennessee River, Coytee, Loudon Co., Tenn.

Walker coll. (Adams).

- | | |
|-----------------------------|------------------------------|
| 1. <i>Fusconaia pilaris</i> | 3. <i>Truncilla haysiana</i> |
| 2. <i>Lampsilis ovata</i> | 4. <i>T. capsaeformis</i> |

HIWASSEE RIVER DRAINAGE.

Spring Creek, Austral, Polk Co., Tenn.

Carn. Mus. (Ortmann, May 23, '15).

- | | |
|---|--------------------------------|
| 1. <i>Fusconaia barnesiana bigbyensis</i> | 3. <i>Eurynia vanuxemensis</i> |
| 2. <i>Eurynia nebulosa</i> | |

Cane Creek, McMinn Co., Tenn.

Walker coll. ("Cane Creek, Monroe Co.;" this is near Etowah, McMinn Co.).

- | | |
|------------------------------------|-------------------------------|
| 1. <i>Fusconaia barnesiana</i> | 3. <i>Pleurobema oviforme</i> |
| 2. <i>F. barnesiana bigbyensis</i> | |

Conasauga Creek, Monroe Co., Tenn.

* = Walker coll.; ‡ = according to Lewis.

- | | | |
|---|---|-------------------------------|
| *1. <i>Pleurobema oviforme</i> | } | *3. <i>Lasmigona badia</i> |
| *‡2. <i>P. oviforme argenteum</i> (also
Lea) | | *‡4. <i>Alasmidonta minor</i> |
| | | ‡5. <i>Eurynia nebulosa</i> |

Ocoee River, Ducktown, Polk Co., Tenn.

Walker coll.

1. *Alasmidonta marginata*

Hiwassee River, Austral, Polk Co., Tenn.

Carn Mus. (Ortmann, Sept. 19, '15).

- | | | |
|-----------------------------------|---|----------------------------|
| 1. <i>Fusconaia barnesiana</i> | } | 5. <i>Lasmigona badia</i> |
| 2. <i>F. barnesiana tumescens</i> | | 6. <i>Eurynia trabalis</i> |
| 3. <i>Pleurobema oviforme</i> | | |
| 4. <i>P. oviforme holstonense</i> | | |

Hiwassee River, Kincannon Ferry, Meigs Co., Tenn.

Walker coll. (Adams, Oct. 9, '01).

1. *Elliptio niger*

Hiwassee River, Meigs Co., Tenn.

Walker coll. (Adams).

1. *Quadrula verrucosa*2. *Lampsilis fasciola**South Chickamauga Creek, Ringgold, Catoosa Co., Ga.*

* = Walker coll. (Adams, Oct. 21, '01); † = Carn. Mus. (Ortmann, May 20, '15).

*†1. *Pleurobema oviforme argenteum*†8. *Medionidus plateolus*†2. *Elliptio dilatatus*†9. *Eurynia trabalis*†3. *Lasmigona badia*†10. *E. nebulosa*†4. *L. costata*11. *Lampsilis ovata ventricosa*
(seen)†5. *Alasmidonta minor*†12. *L. fasciola*†6. *Ellipsaria fasciolaris*†7. *Obovaria subrotunda levigata*

TENNESSEE PROPER, AT AND BELOW KNOXVILLE.

Tennessee River, at and above Knoxville, Knox Co., Tenn.

‡ = according to Pilsbry & Rhoads; † = Carn. Mus. (Ortmann, Sept. 22, '15; B. F. = Brabson Ferry, and D. I. = Dickerson Island).

†1. *Fusconaia pilaris*†13. *Dromus dromas*†2. *F. barnesiana tumescens*†14. *Obovaria subrotunda*†3. *Quadrula pustulosa* (B. F.)††15. *Nephronaias ligamentina gibba*
(D. I.)†4. *Rotundaria tuberculata*††5. *Plethobasus cooperianus* (B. F.)†16. *N. pectorosa*†6. *Pleurobema obliquum* (B. F.)†17. *Plagiola lineolata* (B. F.)†7. *P. obliquum rubrum*††18. *Proptera alata* (B. F.)†8. *P. oviforme holstonense*†19. *Lampsilis ovata*††9. *Elliptio niger* (D. I.)†20. *Truncilla triquetra*†10. *E. dilatatus*†21. *T. haysiana*†11. *Lasmigona costata*†22. *T. propinqua*†12. *Ellipsaria subtenta**Tennessee River, three miles below Knoxville, Knox Co., Tenn.*

Carn. Mus. (Ortmann, Sept. 21, '15).

1. *Fusconaia pilaris* }
2. *F. pilaris lesueuriana* }3. *Quadrula pustulosa*4. *Q. metanevra*5. *Rotundaria tuberculata*6. *Plethobasus cooperianus*7. *Pleurobema obliquum*8. *Pleurobema obliquum rubrum*9. *Elliptio niger*10. *E. dilatatus*11. *Dromus dromas*12. *Nephronaias ligamentina gibba*13. *Plagiola lineolata*14. *Eurynia recta*

Tennessee River, Little River Shoals, Knox Co., Tenn.

* = Walker coll.; ‡ = according to Lewis.

- | | |
|---|--|
| *1. <i>Fusconaia barnesiana tumescens</i> | *6. <i>Lasmigona costata</i> |
| *2. <i>Pleurobema obliquum</i> | *7. <i>Nephronaias ligamentina gibba</i> |
| *3. <i>P. oviforme</i> | *8. <i>Euryntia fabalis</i> |
| *4. <i>P. oviforme holstonense</i> | †9. <i>Truncilla lewisi</i> |
| *5. <i>Elliptio dilatatus</i> | |

Tennessee River, Concord, Knox Co., Tenn.

‡ = according to Lewis; † = Carn. Mus. (Ortmann, Sept. 9, '14).

- | | |
|--|--|
| †1. <i>Quadrula pustulosa</i> | †4. <i>Elliptio niger</i> |
| †2. <i>Rotundaria tuberculata</i> | †5. <i>Strophitus edentulus</i> |
| †3. <i>Pleurobema oviforme holstonense</i> | †6. <i>Nephronaias ligamentina gibba</i> |
| | †7. <i>Euryntia recta</i> |

Tennessee River, Chota Shoals, Knox Co., Tenn.

Walker coll.

- | | |
|---------------------------------------|---|
| 1. <i>Fusconaia cuneolus appressa</i> | 3. <i>Pleurobema oviforme holstonense</i> |
| 2. <i>F. barnesiana</i> | |

Tennessee River (or "Holston River"), Knox Co., Tenn.

(Summary of all species reported from the region between Brabson Ferry and Chota Shoals, mostly without exact locality.)

‡ = according to Lewis; § = reported by Pilsbry & Rhoads; * = Walker coll.; † = Carn. Mus. (Hartman coll. (H.), and Smith coll. (S.)); those reported above are marked: B. = Brabson Ferry; D. = Dickerson Island; K. = Knoxville; L. = Little River Shoals; Co. = Concord; Ch. = Chota Shoals.

- | | |
|---|--|
| †1. <i>Cumberlandia monodonta</i> | †12. <i>Q. intermedia</i> |
| †§2. <i>Fusconaia pilaris</i> —K. | †13. <i>Q. cylindrica</i> |
| ††3. <i>F. pilaris lesueuriana</i> —K. | †§†14. <i>Rotundaria tuberculata</i> —K. Co. |
| †4. <i>F. cuneolus</i> (?) | †§†15. <i>Plethobasus cooperianus</i> —B. K. |
| *5. <i>F. cuneolus appressa</i> —Ch. | †16. <i>P. cyphus</i> |
| †6. <i>F. cor</i> | †*17. <i>P. cyphus compertus</i> (also Frierson) |
| †*7. <i>F. barnesiana</i> —Ch. | †18. <i>Lexingtonia dolabelloides</i> |
| †§*8. <i>F. barnesiana tumescens</i> —K. L. | *†19. <i>Pleurobema obliquum</i> —B. K. L. |
| †9. <i>Amblema plicata costata</i> | †20. <i>P. obliquum cordatum</i> |
| ††10. <i>Quadrula pustulosa</i> —B. K. Co. | †§†21. <i>P. obliquum rubrum</i> —K. |
| ††11. <i>Q. metanevra</i> —K. | |

- | | |
|--|---------------------------------------|
| †*22. <i>P. oviforme</i> —L. | †43. <i>P. fragilis</i> |
| †§*23. <i>P. oviforme holstonense</i> —K.
L. Co. Ch. | †§†44. <i>Proptera alata</i> —B. K. |
| †§†24. <i>Elliptio niger</i> —D. K. Co. | †45. <i>Toxolasma lividum</i> |
| †§*†25. <i>E. dilatatus</i> —K. L. | †46. <i>Lemiox rimosus</i> |
| †26. <i>Lastena lata</i> | †47. <i>Medionidus plateolus</i> |
| †§*27. <i>Lasmigona costata</i> —K. L. | †*48. <i>Eurynia fabalis</i> —L. |
| †28. <i>Alasmidonta marginata</i> | †49. <i>E. nebulosa</i> |
| ††29. <i>Strophitus edentulus</i> —Co. | †50. <i>E. vanuxemensis</i> |
| †30. <i>Ellipsaria fasciolaris</i> | ††51. <i>E. recta</i> —K. Co. |
| †§31. <i>E. subtenta</i> —K. | †§52. <i>Lampsilis ovata</i> —K. |
| †32. <i>Obliquaria reflexa</i> | †53. <i>L. fasciola</i> |
| ††33. <i>Cyprogenia stegaria</i> (H.) | *54. <i>L. orbiculata</i> |
| †§†34. <i>Dromus dromas</i> —K. | †§55. <i>Truncilla triquetra</i> —K. |
| †35. <i>Dromus dromas caperatus</i> | †56. <i>T. arcaformis</i> |
| *†36. <i>Obovaria retusa</i> (S.)—K. | †57. <i>T. interrupta</i> |
| †§37. <i>O. subrotunda</i> —K. | *58. <i>T. lenior</i> |
| †§*†33. <i>Nephronaias ligamentina</i>
<i>gibba</i> —D. K. L. Co. | †§59. <i>T. haysiana</i> —K. |
| †§39. <i>N. pectorosa</i> —K. | ††60. <i>T. stewardsoni</i> (H.) (S.) |
| †40. <i>Amygdalonia truncata</i> | †61. <i>T. lewisi</i> —L. |
| ††41. <i>Plagiola lineolata</i> —B. K. | †§†62. <i>T. propinqua</i> (S.)—K. |
| †42. <i>Paraptera leptodon</i> | ††63. <i>T. torulosa</i> (H.)—K. |
| | ††64. <i>T. capsaeformis</i> (H.) |

Anodontoides ferussacianus, reported by Lewis (as *Anodonta oblita*), has probably been misidentified. Also *Fusconaia cuneolus* is doubtfully given by Lewis; however, it may occasionally turn up in this region.

Tennessee River, Hiwassee Island, Dayton, Rhea Co., Tenn.

Walker coll. (Adams, Oct. 13, '01).

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|-----------------------------------|----------------------------------|
| 1. <i>Amblema plicata costata</i> | 4. <i>Elliptio dilatatus</i> |
| 2. <i>Pleurobema obliquum</i> | 5. <i>Ellipsaria fasciolaris</i> |
| 3. <i>Elliptio niger</i> | |

Tennessee River, Rathburn, Hamilton Co., Tenn.

Walker coll. (Adams).

- | | |
|--|--------------------------------|
| 1. <i>Quadrula pustulosa</i> | 7. <i>Elliptio niger</i> |
| 2. <i>Rotundaria tuberculata</i> | 8. <i>E. dilatatus</i> |
| 3. <i>Lexingtonia dolabelloides</i> | 9. <i>Obliquaria reflexa</i> |
| 4. <i>Pleurobema obliquum cordatum</i> | 10. <i>Cyprogenia stegaria</i> |
| 5. <i>P. obliquum rubrum</i> | 11. <i>Dromus dromas</i> |
| 6. <i>P. oviforme holstonense</i> | 12. <i>Plagiola lineolata</i> |

626 ORTMANN—NAYADES OF UPPER TENNESSEE DRAINAGE.

Tennessee River, Chattanooga, Hamilton Co., Tenn.

‡ = according to Pilsbry & Rhoads; * = Walker coll. (Adams, Oct. 22, '01; † = Carn. Mus. (Juny coll.).

‡1. *Quadrula pustulosa*

*2. *Q. metanevra*

‡3. *Plethobasus cooperianus*

‡4. *Pleurobema obliquum*

‡5. *P. oviforme holstonense*

‡6. *Elliptio niger*

‡7. *Elliptio dilatatus*

‡8. *Ellipsaria fasciolaris*

‡*9. *Dromus dromas*

‡10. *Nephronaias ligamentina gibba*

†11. *Truncilla torulosa*

BRIEF NOTES.

By BENJAMIN SMITH LYMAN.

(*Read March 1, 1918.*)

SOUL.

In the infancy of the human race, grown men, of course, had the ideas of little children. As the eye and the sensory nerves perceive the bodily actions and experiences, nearly the same as if those of another body, so the invisible actions and experiences of the brain are observed by the pineal gland or some other parts of the brain, seemingly by a separate organ, or almost with the appearance of the observer's being a distinct individual. The child-like early men evidently so reckoned it, and, while making the observation by their own brain, without conscious effort, considered the observer to be separate from their body. This retired, refined observer of the actions of their body and, to some extent, of their brain, they called their soul, and imputed to it a separate existence, and, in some tribes, a life beyond the life of the body, as suggested by apparitions and dreams. As the idea was fundamentally child-like, it was readily absorbed by children, and with increasing years was tenaciously retained. It did not seem inconsistent with the action of the invisible wind and perhaps other actions of an invisible source. The ancient Latin word for soul is even plainly derived from the word for breath, showing that the soul was, in action, or originally, like air, or the wind. In the course of time, the tenaciously held idea of the soul has become more refined; and, while the soul is still evidently taken to be a material substance, it is quite etherially, tenuously refined, and is often spoken of as altogether immaterial. Nevertheless, it always has, when sifted, undeniably several of the characteristics of concrete matter.

As late as medieval times, each human body was conceived to have not only one, but at least three, souls. As the Right Reverend Avitus, in the sixth century, elucidated:

"Of Man, flesh, spook, mind, spirit, in all twice twain,
 To places four these double pairs attain :
 To earth the flesh ; the spook near by will fly ;
 The mind to Netherworld, the spirit soars high."

Or in the original :

"Bis duo sunt Homini, manes, caro, spiritus, umbra ;
 Quatuor ista loci bis duo suscipiunt :
 Terra tegit carnem, tumultum circumvolat umbra,
 Orcus habet manes, spiritus alta petit."

According to Hindoo belief, each body has seven souls. Of course, one of the souls would be suggested by the lifelike apparition of deceased relatives or friends, seen either while the observer was awake or in dreams. The absurdity of the inference from the occurrence is evident from the fact that the apparitions reproduce even the inanimate clothing, as well as the admittedly mortal material body.

The idea of a soul has lent itself very readily to the promotion of morals, so dear and so natural to the human race. The soul in its life after the death of the body has been supposed to be in happy or unhappy condition, according to behavior during the life of the body ; or according to the behavior of descendants left alive ; supplying an incentive to good behavior during one's own life, or after the death of loved relatives. The systems of morals built upon the idea of a soul are highly refined, with marvellously ingenious and carefully consistent complications ; and are considered to be a strong argument in favor of that idea. But, as all false errors are pernicious, and entail further harmful errors ; so, we may be sure, the eradication of this falsity would be a benefit to morality. The strongest incentives to morality and the surest guides to it are to be found in the relations of the natural body, without regard to any imaginary soul ; and morality based upon the existence of souls is uncertain and groping, notwithstanding its good intention.

THE WORD OF GOD.

The Christian, Buddhist and other peoples so deeply revere their sacred scriptures, that they downright consider them to be literally the word of God, an omniscient God. But that idea is hardly borne

out by the internal evidence. An omniscient god would speak with yet greater wisdom than the wisest man. A wise lawyer exerts his utmost skill to express his meaning clearly and simply, beyond the possibility of misunderstanding, or of twisting, avoiding hyperbole, or any kind of exaggeration, or possible obscurity. We do not find such language in the gospels; and, indeed, it would be altogether foreign to their Asiatic authorship. We find there quite seriously the monstrous hyperboles of swallowing a camel, of having a wooden beam in the eye, of a camel's going through the eye of a needle, of heaping coals of fire on the head; all well enough as jokes, like the description of the Green Mountain road so steep that "greased lightning could not go down it without the breeching on." But the free use in earnest of such expressions suggests a like absence of literal meaning for other words, such as the removal of a mountain by sufficient faith. The trouble comes when it is to be decided where such free interpretation shall be applied. Is it meant to be taken literally that we should swear not at all; that, when we are struck on one cheek, we should turn the other cheek; that we should out and out love our enemies; that we should exactly do to others what we wish them to do to us? The general secular decision in Christendom on such points has been that the injunctions were not to be taken altogether literally. Yet many simple, honest, straightforward individuals have been inclined to insist that the expressions should be taken literally; for the word of God could have been uttered only in a strictly literal sense, not to be in any way perverted or twisted.

CLASSICAL EDUCATION.

Much has justly been said of the beneficial effect of the cultivation of literary taste and of the enrichment of the mind from acquaintance with classical books, masterpieces that have outlasted many centuries; and something has been said of the advantage of classical linguistic knowledge. But too little seems to have been said of the logical downright need of studying the classics as a help towards a thorough understanding of our own language, and towards easy and correct reasoning.

What most distinguishes a man from a brute? It is, of course, the reasoning power. And what gives the power to reason? Clearly, it is language, the means by which reasoning is done. The cultivation of the power of language, how to use it readily and accurately, is, then, of the highest importance. With our English language, derived in so large a part from the classical languages, it seems quite plain that a full understanding of it would be greatly aided by a good knowledge of them. Thereby, the true significance of words would be learned, their precise shades of meaning, their original meaning, and the meaning that has been historically acquired. Evidently, the most perfect knowledge of the meaning of words would be gained by a study of their use in their original classical languages. With a thorough knowledge of the meaning of words, they could readily be used correctly in reasoning. The danger of fallacies would in great measure be avoided. Some such knowledge could be learned from English etymological grouping, or dictionaries; but obviously much more satisfactorily by studying the classics and their languages.

OF.

At the age of nine years, my budding philological inclination was bluntly rebuffed and checked by a reminder of my complete ignorance of the meaning and etymology of even so small a word as *of*. It has become clear that the word is closely allied to *off*, and that it signifies that one thing may be considered concretely or abstractly to be off from, or a part of, another thing. But a knowledge of the precise meaning of the word does not seem to be universal, and the word seems consequently to be inaccurately used. One source of error is the impression that the word is the precise equivalent of the French *de*; so that a supposedly literal translation would sometimes introduce a Gallicism into our English. But the French *de* is derived from the Latin *de*, and means concerning, quite a different meaning from our word *of*. The meaning of *de* is much more correctly indicated by our adjectival relation of two substantives. The French *école de danse* becomes dancing school; *école des mines* becomes mining school, or mine school, a school in regard to mines, not of mines, concretely or abstractly off from

mines. The instinct in the matter is much stronger and more correct in England than in America. The English quite naturally say correctly, Public Works Department, while in America, we sometimes, as a result of dangerous little knowledge, meet with Department of Public Works, that is, intended as a literal translation from the French, which would be literally department concerning public works. The adjectival relation gives practically the same meaning, showing that the department is the one concerned with public works, not of them (which would be one of them, not including them all). The difference is: a department that has to with all the public works; and a department among (or off from) public works.

SOLDIERS' AND SAILORS' INSURANCE.

By SAMUEL McCUNE LINDSAY, PH.D., LL.D.

(Read April 20, 1918.)

Among all the marvelous applications of science to warfare which the great European war has produced,—the gas shell, the 75-centimeter gun, the submarine, the Liberty motor, etc,—there is nothing more significant than the attempt to apply the principles of mutuality and insurance to lighten the burdens of war for our fighting men and their families and dependents. As soon as America entered the European war and undertook to do its part, we realized that for the protection of those who must go to the front the existing pension legislation and the old six months gratuity act were as much out of date as the flint-lock musket. Within the first six months after the United States declared war on Germany, Congress worked out and enacted the War Risk Insurance act, which in another six months, or at the end of the first year of our participation in the war, has made the United States Government the greatest life and casualty insurance company in the world. At the close of business yesterday (April 19, 1918) in the matter of insurance liability alone, the War Risk Bureau had accepted 1,785,173 applications for insurance on the lives of soldiers and sailors, in amounts of not less than \$1,000 nor more than \$10,000 upon any one such life, aggregating \$14,542,471.500.¹ This is more outstanding life insurance for the United States Government than the combined outstanding life insurance carried by the twenty largest companies in America, and it is nearly two and one half times the total amount of life insurance written during the previous year by all of the companies in the United States. Probably at least 95 per cent. of all the fighting men of the army and navy who are eligible to take this insurance have been covered and the average amount per man on April 19 was \$8,146. The average day's business of this in-

¹ For corresponding figures revised to Aug. 20, see below, p. 647.

surance bureau is \$100,000,000, or more than the total outstanding business of many a good insurance company after many years of successful business experience.

The benefits conferred by insurance are only part of those provided by this law and intended to safeguard the welfare and morale of our army and navy. The War Risk Insurance Law of October 6, 1917, is in reality three great measures in one. It provides for three new, effective and far-reaching services of the federal government, namely: (1) Allotments of pay and family allowances; (2) compensation and indemnity for death or disability; (3) insurance for death or total disability. All three services, each of which represents a huge undertaking on the part of the government, are so combined and intertwined as to provide a scientific, comprehensive, adequate and just measure of community support and concern for the economic security and future welfare of those families, which provide the men privileged to do the fighting in this war. Taken together these provisions for what has generally become known as war risk insurance will render any general system of pensions antiquated, unfair and wholly unnecessary.

In September, 1914, only a little over a month after the beginning of the European war, Congress established by act of September 2, 1914, a Bureau of War Risk Insurance in the Treasury Department, clothed with authority and charged with the responsibility of insuring American ships and their cargoes, at rates which private carriers could not afford, in order that the commerce of a neutral nation might be maintained on the high seas. On June 12, 1917, Congress extended the authority of this bureau and authorized it to provide for the issuance of insurance against war risks on masters, officers and crews of merchant vessels. On these foundations, Congress by the act of October 6, 1917, created in this Bureau of War Risk Insurance a division of Military and Naval Insurance. A division of Marine and Seamen's Insurance was also established to attend to the previous business of the Bureau. The new division began the administration of the new scheme for allotments and allowances, compensation and insurance for soldiers and sailors. Over 3,000 employees² are required to handle the work of this new

² On July 1, 1918, there were 8,000 employees required to take care of this work in the Bureau of War Risk Insurance.

division alone and the volume of its business has not yet reached its maximum proportions.

Permit me now briefly to describe the three subdivisions of this beneficent law and to summarize its workings, problems and results during the first six months of its history.

I. ALLOTMENTS OF PAY (COMPULSORY AND VOLUNTARY) AND FAMILY ALLOWANCES.

Congress had prepared the way and laid the right foundation for allotments and allowances by raising the pay of enlisted men in the Army and Navy, making the minimum pay for nearly all in the service \$30 a month, or double what it was before in most cases, and higher than that of any other army in the world. This was a just measure to protect the highest standards of living in any country when so many of our citizens were called upon to forsake their usual peaceful occupations. But this was not enough to equalize the sacrifices which all citizens must make in time of war. No rate of pay for the army and navy could be made high enough to do that. So Congress proceeded to supplement the regular pay upon the theory that since the call to arms does not annul the moral and legal obligations of every man to support his family and those who have a blood-tie claim upon his earnings, it is the plain duty of the whole country which he serves to aid him financially to do this without undue lowering of his standard of living, and without requiring a disproportionate sacrifice on the part of his dependents.

This is sound doctrine, however, only when the enlisted man first does his part and contributes from his own resources all he can reasonably spare. Therefore we begin with the allotment which must precede a request for an allowance. Allotments and family allowances are not provided for commissioned officers or for members of the Nurse Corps (female). The allotment is compulsory for every enlisted man who has a wife, or child under eighteen years of age or of any age if the child is insane or permanently helpless, or a divorced wife to whom alimony has been decreed by a court, and who has not remarried. These persons constitute what is known as "Class A" dependents. A common-law wife is entitled to the same consideration as a legal wife and the claims of a legal wife and of

all children take precedence of those of a divorced wife. Every enlisted man is required to file with the War Risk Bureau a statement, for which an allotment and allowance blank is furnished, showing whether or not he has any dependents, and if so how many, and what are their blood or marriage relationships to him.

Nearly a million and a half such statements are now on file in the War Risk Bureau and about 830,000 of them claim that they have no dependents for whom allotment of pay is compulsory or for whom they wish to make a voluntary allotment. Some of these no doubt will be found to have a wife or child for whom they seek to evade responsibility, and such wife or child or some one on their behalf should make application direct to the bureau if they do not receive the allotment and the man will be brought to account. If an allotment is made for any beneficiary and through inadvertence or otherwise no request has been made for a family allowance, the wife, child or beneficiary, or some one on their behalf, should apply to this bureau for the family allowance. Some will later want to make voluntary allotments for Class B dependents when perhaps they find it more convenient to do so. Class B dependents for whom the allotment is voluntary include parents, brothers, sisters and grandchildren. Parents include grandparents and step-parents either of the person in the service or of the spouse.* Brothers and sisters include those of the half blood and step-brothers and step-sisters and brothers and sisters through adoption. Even if Class B dependents are in want, an enlisted man is not compelled to make an allotment for their support, but he must do so before the government will pay any family allowance to them.

The allowance in all cases both for Class A and Class B dependents is granted only when applied for, after the necessary amount of allotment of pay has been made.

The allotment must in practically every case where an allowance is asked for be at least \$15 per month, and must equal the amount

* An Act of June 25, 1918, amended the definition of the term "parent" so as to make it include a father, mother, grandfather, grandmother, father through adoption, mother through adoption, step-father, step-mother, either of the person in the service or of the spouse.

of the allowance which the government is asked to give, provided such amount is not more than half the monthly pay.⁴

Where a man has Class A dependents but no Class B dependents, he must allot at least \$15 per month and as much more up to half his pay to equal the allowance requested according to the following schedule: for a wife but no child, \$15; a wife and one child, \$25; a wife and two children, \$32.50, with \$5 per month additional for each additional child up to a total of \$50, which is the maximum government allowance to the dependents (Classes A and B) of any one man under all circumstances; no wife but one child, \$5; two children, \$12.50; three children, \$20; four children \$30, and \$5 for each additional child. These allowances to Class A dependents are made without reference to dependency or need except that they may be waived by a wife who gives evidence of sufficient means for her own support, but may not be waived by a child, and a man may be exempted in certain exceptional circumstances from making a compulsory allotment.

When a man in the service has Class A dependents for whom he is making an allotment and in addition has Class B dependents for whom he wants an allowance he must make an additional allotment equal to one seventh of his pay. Under exceptional circumstances this additional allotment may be waived by the bureau. Class B dependents receive allowances as follows: one parent, \$10; two, \$20; each grandchild, brother or sister, or additional parent, \$5, provided the total family allowance for Classes A and B dependents for one man does not exceed \$50 per month.

As there are no compulsory allotments for a woman in the service, her dependents are always Class B dependents. For Class B dependents where there are no Class A dependents men and women alike in the service must allot, if they want allowances for their Class B dependents, an amount not less than \$15 per month, and

⁴ By an amendment (Act of June 25, 1918), the allotment requirement has been greatly simplified, and is now a flat compulsory allotment of \$15 per month, regardless of the amount of pay or the amount of the allowance requested, for every man with Class A dependents and an additional allotment of \$5 per month for Class B dependents (or \$15 if he has no Class A dependents) if he requests an allowance for Class B dependents. This fixed flat allotment for either Class A or Class B avoids the necessity for the frequent changes due to changes in pay.

equal to the allowance which the government will give, provided such amount is not more than half the monthly pay.⁵ Women receive for children, who would be Class A dependents for men, allowances as follows: one child, \$5; two children, \$12.50; three children, \$20; four children, \$30, with \$5 per month for each additional child.

Class B allowances are subject to two conditions: (1) The person receiving the allowance must need it and be dependent in whole or in part for support upon the person making the allotment. They need not be wholly dependent. They may have earnings of their own or also other sources of support. (2) The total of the allotment and the allowance paid to the dependents must not exceed the amount of the habitual contribution from the man to the dependents in all cases where dependency existed prior to enlistment or prior to October 6, 1917. Otherwise the government allowance will be proportionately reduced.

The total of the allotment and family allowance for a divorced wife may not exceed the amount of the alimony decreed.

The War Risk Bureau, in its regulations made under the authority of the Secretary of the Treasury, has sought to interpret and apply the law in the broadest and most sympathetic way. For example, the regulation which defines dependency says:

For the purposes of the War Risk Insurance Act, a person is dependent, in whole or in part, upon another, when he is compelled to rely, and the relations between the parties are such that he has a right to rely in whole or in part on the other for his support.

Also, if a Class B dependent, for whom a family allowance is claimed, becomes dependent in whole or in part on the enlisted man, subsequent to both enlistment and October 6, 1917, the limitation as to habitual contributions is regarded as not applicable, and the family allowance is paid without regard to it.

Family allowances are payable for one month after a man is discharged from the service, but are not provided for more than one year after the termination of the war.

⁵ This has been amended by the Act of June 25, 1918, providing for a flat additional allotment of \$5 in all cases where there is an allotment of \$15 for Class A, and a flat allotment of \$15 where there is no allotment for Class A.

The conditions of dependency and habitual contribution make investigation to prevent fraud, and adjustment to the changing conditions affecting dependents, such as births and deaths in the family, children reaching the age of eighteen, or contracting marriage before that age, and economic conditions affecting the family income, of the greatest complexity and difficulty in maintaining the necessary records in the War Risk Bureau in order that awards may be made promptly and allowances paid accurately each month as they become due. Severe penalties are provided for intentional fraud. Anyone knowingly making a false statement of a material fact in connection with claims under the act is guilty of perjury and will be punished by a fine up to \$5,000, or by imprisonment up to two years, or both. A beneficiary, whose right to payments under the act ceases, and who fraudulently accepts such payments thereafter, will be punished by a fine up to \$2,000, or by imprisonment up to one year, or both.

Only great loyalty and patriotism on the part of several thousand employees of all grades has made it possible to establish a new organization, housed in several different buildings, working under the greatest physical limitations under present circumstances in Washington, and to get this work reasonably well started.

Within the first four months after family allowances became payable, over a million checks have been sent out, aggregating more than \$18,000,000 for allotments and \$11,000,000 for allowances. Over a million index cards have been prepared and properly filed, and only 15,000 applications were held in suspense at the end of this period for further correspondence and investigation before awards were made.

Delays have been inevitable. The government has had to rely upon outside agencies to tide over cases of need until its relief could be made effective. The patience of many beneficiaries whose claims could not be adjusted as promptly as the government desired, has doubtless been taxed. The difficulties of making records or getting information concerning men scattered all over the world, in military camps, in the expeditionary forces, and on ships at sea, can not be fully appreciated by every family whose interests naturally seem to them to be of paramount importance. The work is rapidly being

brought under efficient business control, and most of the difficulties, delays and mistakes of the first four months are not likely to continue long.

II. COMPENSATION FOR DEATH OR DISABILITY.

The application of the principles of mutuality and insurance to the risk of death or disability resulting from personal injury suffered or disease contracted in the line of duty, and not due to wilful misconduct on the part of the injured person, is not new. It has been successfully tried out on a large scale through the admirable workings of the national and state workmen's compensation laws now operative for the civilian employees of the federal government and for the industrial workers of 36 states of the American Union. These laws have largely displaced or superseded the old employers liability remedies for industrial accidents. They have proven themselves to be increasingly satisfactory to employers and employees alike. They operate also to place on each industry the cost of the financial burden of its unavoidable industrial accidents as far as that burden can be translated into dollars and cents. They also operate to distribute among the consumers of the goods produced, the cost of industrial accidents incurred in their production to the extent of providing for the payment of a sum proportionate to the loss of earning power and a fair recompense for the suffering that an industrial accident causes the individual workman and his family. They also operate to encourage industry to adopt and develop every possible safety device for the elimination of preventable accidents. The analogy of this industrial experience with compensation remedies to the problem of caring for the hazards of war is plain. In the case of our military and naval forces the industry is an "extra hazardous" one, the payment of compensation must be liberal, the cost will be heavy, the government of the United States is the employer and the nation—the whole people—are the consumers or those for whom the operations of war are carried on. The government therefore should bear the whole cost of compensation for death or disability for officers as well as for enlisted men, and for members of the Nurse Corps (female), and distribute the burden through taxation. It does not require any contribution from the

beneficiaries as it does in the case of allotments of pay upon which family allowances are based or in the case of premiums covering the peace rates for insurance. The soldier or sailor does his part when he risks his life and bears the unavoidable personal suffering from injury or disease incurred in the service of his country. Compensation is a payment in addition to regular pay, family allowances and insurance benefits, and serves to equalize the burdens and risks of military service which are inevitably unequally distributed between those called upon to serve in front line trenches as compared with those serving in no less necessary operations behind the lines.

This second great service of the War Risk Insurance law, which makes provision for compensation for death and disability, is necessarily a complicated and technical one and I cannot attempt here to describe it fully, but only in its general outlines. It is more liberal and far more just than any pension law that has ever been passed or now exists, and it should make any supplementary pension legislation for those engaged in this war wholly unnecessary. While it will cost the government huge sums of money, depending upon the number of men engaged in this war, the length of the war and the severity of our casualties, it will doubtless cost less, be far more just and equitable in its benefits, and give more aid and comfort where it is needed than any general pension scheme could possibly provide.

Compensation for death or disability is provided for all members of the United States Military and Naval Forces, including not only enlisted men but also commissioned officers and members of the Army and Navy Nurse Corps (female). The only person entitled to receive compensation for disability is the man himself. In the case of his death, the widow, child and dependent mother receive the benefits provided. Compensation is not paid automatically, but must be applied for on blank forms furnished by the Bureau of War Risk Insurance. It varies in amounts from \$30 to \$100 a month paid to the disabled man, and from \$20 to \$75 a month paid to his widow, child or widowed mother. Unlike individual compensation the amount does not vary in proportion to the wage or previous income of the disabled person or of the deceased. It is based on a new principle, namely, that of the family need, on the theory that

under the conscription law the family is conscripted when the bread winner is taken away. Therefore, the amount paid, if the man is disabled in the line of duty, varies according to the size of his family and changes from month to month or year to year as the family status changes. If a man is a bachelor and is totally disabled, he gets \$30 a month; if he has a wife but no child living, \$45 a month; a wife and one child, \$55; a wife and two children \$65; a wife and three or more children \$75; no wife but one child living \$40, with \$10 for each additional child up to two; a widowed mother dependent upon him for support in addition to the above amounts, \$10. He is also entitled in addition to free medical, surgical and hospital service and supplies, including artificial limbs, etc., as the director of the War Risk Bureau may determine to be useful and reasonably necessary, and for certain claims of disability such as the loss of both feet, or hands, or both eyes, he gets, in lieu of all other compensation, the flat sum of \$100 a month.

Partial disability is pro-rated at a percentage of the compensation for total disability equal to the degree of the reduction in earning capacity, resulting from the disability.

In case of death resulting from injury in the line of duty, the monthly compensation paid is as follows: For the widow alone, \$25; for the widow and one child \$35; for the widow and two children \$47.50 with \$5 for each additional child up to two; if there be no widow then for one child \$20; for two children \$30; for three children \$40 with \$5 for each additional child up to two; for a widowed mother \$20, except that the amount paid to a widowed mother when added to the total amount payable to the wife and children does not exceed \$75.

Compensation is payable for the death of but one child. No compensation is paid to a widowed mother on account of a child if she is already in receipt of compensation on account of the death of her husband.

Compensation is further limited by the following considerations: None is paid if the injury or disease was caused by the man's own willful misconduct. None is paid for death or disability occurring later than one year after the man leaves the service, unless a medical examination at the time of his resignation or discharge or within

one year thereafter proves that the man was then suffering from an injury or disease likely to cause death or disability later. None is paid for death inflicted as punishment for crime or military offence unless inflicted by the enemy. None is paid unless the claim is filed within five years after the death was recorded in the department in which the man was serving at the time of his death, or in case of death after discharge or resignation from service, within five years after death. None is paid for disability unless the claim is filed within five years after discharge or resignation from the service or within five years after the beginning of disability occurring after leaving the service. None is paid for any period more than two years prior to the date of claim. None is paid during the period in which the man is reported as missing, if during that time his pay and family allowance go on; a man is not considered dead until reported so by the department under which he is serving. None is paid to those receiving service or retirement pay. Dishonorable discharge terminates the right to the compensation. Compensation is not assignable and is exempt from attachment, execution and from all taxation, and the law providing for gratuity of payments for death in the service and all existing pension laws do not apply to persons in the service at the time of the passage of this act, or to those entering into the service after, or to their widows, children or dependents, except insofar as rights under such laws shall have heretofore accrued. In addition to the benefits mentioned there is provision for the payment by the United States of burial expenses not to exceed \$100. The compensation to a widow or widowed mother ceases upon her remarriage, and to a child when it reaches the age of eighteen years or marries, unless the child be incapable because of insanity, idiocy, or being otherwise permanently helpless, in which case it continues during such incapacity.

In the interpretation of the compensation provisions the Bureau of War Risk Insurance has endeavored to be as liberal as the spirit of the law permits. An illustration of this is found in the definition by regulation of "total disability" which is broadly defined as "an impairment of the mind or body which renders it impossible for the disabled person to follow a gainful occupation" and again in the regulation which says that "total disability is deemed to be perma-

ment whenever it is founded upon conditions which render it reasonably certain that it will continue throughout the life of the person suffering from it."

In addition to providing compensation for disability and death, the government promises in this act to do everything in its power to restore a man who has been injured, by accident or disease incurred in the line of duty, to the fullest possible physical and economic power. The people of the United States do not want this war to produce a large crop of "corner loafers," that is men who will come back, injured more or less seriously by their war experience and without ambition, to rely upon what the government will do for them and consider that it owes them a living. They will be far happier if they can be restored in part, if not in whole, to their previous earning ability and have found for them some new occupation which they can successfully pursue even though maimed and impaired in physical powers. Courses of education and rehabilitation will be provided by the United States. The act plainly authorizes the Bureau of War Risk Insurance to make it possible for men to avail themselves of such training, even if some method of re-enlistment in the military or naval service may be necessary by which they will receive full pay as of the last month of active service while following such courses of training and rehabilitation. It also authorizes the bureau to withhold the payment of compensation during such period as the person to whom it has been awarded willfully fails to follow such course of training or rehabilitation as may be prescribed.

III. INSURANCE AT ATTRACTIVE RATES.

The third great service of the War Risk Insurance Bureau is destined to copper-rivet the benefits of the other two, that is of the family allowances and the compensation, and also to stimulate and reward economic foresight and individual initiative on the part of our fighting men. The government insurance, offered in amounts of not less than \$1,000 or in multiples of \$500 up to not more than \$10,000, is voluntary. It may be taken, however, by every commissioned officer and enlisted man and every member of the army nurse corps (female) and of the navy nurse corps (female) when

employed in active service under the War and Navy departments. Its purpose is twofold—first, to restore a man's insurability which was either taken away from him or considerably impaired the moment he entered the military or naval service; secondly, to afford our fighting forces protection for themselves and their dependents additional to and greater than is provided by the compensation provisions of this act, without medical examination and without cost for solicitation, advertising or administrative expenses,—the usual overhead charges with which commercial insurance premiums are loaded. The government offers at peace-rate cost this insurance and whatever the war risk, due to military service, may be, the government assumes that, pays it and presents it to every man in its military or naval forces who elects to take the insurance. How well the men have appreciated this offer is shown by the fact that probably 95 per cent. of those eligible to take the insurance have done so and the amounts they have elected to take have averaged well over 80 per cent. of the maximum allowed. The predictions of practically all persons experienced in the insurance business have been utterly confounded by this result obtained without the services of personal solicitors. Both Congress and the bureau were assured that we need not expect more than half of the total number of men eligible to take any insurance at all and of those that did, probably most of them would take small amounts so that the average would not exceed 20 to 25 per cent. of the maximum allowed.

The insurance then is term insurance at peace rates with premiums payable in monthly installments which brings it well within the reach of the poorest paid soldier, who, even after making a compulsory allotment of \$15 per month in order to secure a family allowance for his wife and children or a voluntary allotment of the same amount for other relatives dependent upon him in case he has no wife or children, for an additional sum of approximately \$6.50 per month may secure \$10,000 of insurance (the maximum he is allowed to take) and still have \$8.50 per month for spending money, or with minor additions or the extra pay allowed in foreign service, he may have approximately \$10 per month for his own use, which in the opinion of the commanding officers of our military and naval forces, is more than enough to meet every legitimate need.

The insurance is automatically renewed from year to year at the slightly increased premium rate for each additional age year until it lapses automatically five years after the end of the war, unless within that five years the insured exercises his option of converting it without physical examination into any of the ordinary forms of insurance at the rates which the government may prescribe. The premium rates are based upon the American experience table of mortality, with interest at $3\frac{1}{2}$ per cent. per annum. The insured, therefore, gets his insurance in an extra-hazardous occupation at less cost than it would cost him in peace times in any commercial insurance company. He has 120 days after enlistment, or after entering the active service, in which to elect to take insurance and to decide upon the amount he wants. He may drop any part of his insurance which he does not wish to carry at any time he chooses, but at the expiration of the 120-day period he may neither take insurance in case he has not elected previously to do so, nor increase the amount of his policy in case he has not elected to take the maximum of \$10,000 allowed. Premiums are usually paid automatically by monthly allotment of pay, and the insurance runs as long as the premiums are paid, whether the man leaves the service or not, unless it is terminated by the discharge or dismissal of any person from the military or naval forces on the ground that he is an enemy alien, conscientious objector, or a deserter, or is guilty of mutiny, treason, spying, or any offense involving moral turpitude, or willful and persistent misconduct.

The amount of the policy in the event of death or total and permanent disability is payable in 240 equal monthly installments, except that if the insured is permanently and totally disabled and lives longer than 240 months, the monthly payments at the 240 months' rate continue as long as he lives and is so disabled. In the event of the death of the insured before 240 monthly payments have been made the remaining monthly installments go to his beneficiary. In the event of death before any or all of the 240 monthly payments have been made, the insurance is payable in 240 equal monthly installments to any beneficiary designated by the insured within the limited class of beneficiaries prescribed in the law, which includes a spouse, child, grandchild, parent, brother or sister as defined and

explained above in the discussion of allotments, allowances and compensation. If no beneficiary within the permitted class has been designated by the insured, or if the one so designated does not survive him, the payments go to such persons within the permitted class of beneficiaries as would be entitled, under the laws of the state of the residence of the insured, to his personal property in case of intestacy and if no such person survives the insured, an amount equal to the reserve value, if any, of the insurance at the time of death of the insured, calculated on the basis of the American experience table of mortality and $3\frac{1}{2}$ per cent. interest, is paid to the estate of the insured in full for all obligations under the contract of insurance.

There are no provisions for lump sum payments. Insurance payments are further protected, as are also payments of allotments, family allowances and compensation, in that they are not assignable nor subject to the claims of creditors of any person to whom an award is made, except for claims of the United States against the person on whose account the allotments, family allowances, compensation or insurance are payable.

An interesting provision was made for automatic insurance of a limited amount and somewhat more restricted in its benefits to cover all men in the active service from the date of the beginning of our participation in the war (April 6, 1917), who, during the 120-day period immediately following the publication of the terms and conditions of this insurance (October 15, 1917) were totally and permanently disabled or died without having applied for insurance. The act specified that all such men were to be deemed to have applied for and to have been granted insurance payable to such person during his life in monthly installments of \$25 each, which was the equivalent of approximately \$4,500 of insurance.

In the event of death the payments of the balance of 240 monthly installments at \$25 each were to be made to beneficiaries, restricted, however, to a widow remaining unmarried, a child, or a widowed mother.⁹

⁹ This restriction with respect to the beneficiary of automatic insurance was amended by the Act of June 25, 1918, so that the beneficiary might be a widow during her widowhood, or if there is no widow surviving, then the

Reference has already been made to the remarkable response made by the military and naval forces to the offer of this voluntary insurance. The actual figures (corrected to August 20, 1918) show that the Bureau of War Risk Insurance has received and accepted in the first ten months of its operation, 3,319,593 applications for twenty-eight and a half billions of dollars of insurance, which averaged \$8,602 per application. As in some instances more than one application was made on behalf of an enlisted man, the total number of applications on August 20, which is probably greater than the total number of men in the military and naval forces on that date, does not represent the exact number of persons insured, and the average amount of insurance taken per person is therefore greater than \$8,602.

This huge government insurance business represents more outstanding insurance in the first year of its history than that of any other insurance organization in the world and more than the total life insurance written during the past year by the twenty largest companies in the United States. A single day's business, for example, that of August 20, amounts to twenty-seven thousand applications for a total of over two hundred sixty-seven million dollars, or more than the total outstanding business of many a good-sized private insurance company.

Voluntary insurance supplied by the government at cost is a service of the greatest social significance. Combined with the benefits of family allowances and of compensation for death and disability, it provides in a scientific, just and equitable way for the fulfillment of a great national obligation which is intended to safeguard the morale of our Army and Navy and of those families of the nation which are making the greatest sacrifices for the successful prosecution of the war. The War Risk Insurance Act in its entirety is for the American people a new departure of the greatest significance as an expression of a new sense of social solidarity and unity of national purpose. Other nations have experimented for

child or children of the insured, or if there is no child surviving, then the mother, or if there is no mother surviving, then the father, if and while they survive the insured; and this provision was made retro-active and the Bureau of War Risk Insurance directed to revise all its awards of automatic insurance on July 1, 1918, in accordance with these amended terms.

many years with the principles of social insurance in the solution of some of their most difficult social problems. The United States has now started upon the same road, and in the War Risk Insurance Act is breaking new ground in some directions not yet undertaken by any other nation. The successful administration of this remarkable legislation, which is confidently anticipated in spite of many initial difficulties, will mark a new era in our history, a new stage in social progress and a new chapter in the development of world democracy.

COLUMBIA UNIVERSITY,
NEW YORK, APRIL, 1918.

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1. The candidate shall, on or before November 1, 1918, deliver free of postage or other charges, his discovery, invention or improvement, addressed to the President of the American Philosophical Society, No. 104 South Fifth Street, Philadelphia, U. S. A., and shall distinguish his performance by some motto, device, or other signature. With his discovery, invention, or improvement, he shall also send a sealed letter containing the same motto, device, or other signature, and subscribed with the real name and place of residence of the author.
2. Persons of any nation, sect or denomination whatever, shall be admitted as candidates for this premium.
3. No discovery, invention or improvement shall be entitled to this premium which hath been already published, or for which the author hath been publicly rewarded elsewhere.
4. The candidate shall communicate his discovery, invention or improvement, either in the English, French, German, or Latin language.
5. A full account of the crowned subject shall be published by the Society, as soon as may be after the adjudication, either in a separate publication, or in the next succeeding volume of their Transactions, or in both.
6. The premium shall consist of an oval plate of solid standard gold of the value of ten guineas, suitably inscribed, with the seal of the Society annexed to the medal by a ribbon.

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Vol. LVII.

1918.

No. 7.

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PHILADELPHIA
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1918

American Philosophical Society

General Meeting—April 24-26, 1919

The Annual General Meeting of The American Philosophical Society will be held on April 24th, 25th, and 26th, 1919, beginning at 2 P. M. on Thursday, April 24th.

Members are requested to send to the Secretaries, at as early a date as practicable and before March 19, 1918, the titles of papers which they intend to present so that they may be announced in the *preliminary* programme which will be issued immediately after that date and which will give in detail the arrangements for the Meeting. It is understood that papers offered are original contributions which have not been theretofore presented.

The Publication Committee, under the rules of the Society, will arrange for the immediate publication of the papers presented in either the *Proceedings* or the *Transactions*, as may be designated.

I. MINIS HAYS
ARTHUR W. GOODSPEED
HARRY F. KELLER
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Secretaries

Members who have not as yet sent their photographs to the Society will confer a favor by so doing; cabinet size preferred.

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A BRIEF HISTORY OF THE STUDY OF GREEK VASE-PAINTING.

By STEPHEN BLEECKER LUCE.

(Read April 19, 1918.)

The subject of this paper needs no apology, for the study of Greek vase-painting is of the highest importance to the classical archæologists and philologist.¹ Their appeal is wide, and includes within the scope of their influence not only lovers of the classics, but all who love art and beauty. In the first place, they are all that we have left of the Greek painting of the Age of Pericles. This makes them at once of immense importance to the archæologist, who tries with their aid to reconstruct in his mind the masterpieces of Polygnotes and Zeuxis. To the philologist and the lover of literature, they are valuable as portraying the stories of mythology and history, often being far earlier than our extant literary sources for the myths they represent; to the student of manners and customs, the scenes from private life that they show are of supreme importance; while the archæologist finds pleasure and profit, not only from these things, but from the study of their chronology and technique. It has been truly said that the value of Greek vases is fourfold—ethnological, historical, mythological and artistic.²

This paper deals with an attempt to bring together, in a brief and usable form, the history of the study of these painted vases as works of art and monuments of antiquity from the beginnings of archæological research till the present day. This has been done before,³ but it seems to me that there is need of bringing together the

¹ I shall not discuss in this paper the chronology of the Minoan pottery of Crete, or the history of the discoveries of Evans at Knossos and Schliemann at Mycenae; for the culture that produced this civilization of prehistoric times is entirely different from that of the Hellenes, and is probably non-Greek.

² H. B. Walters, "History of Ancient Pottery," Vol. I, pp. 10-16.

³ Walters, *loc. cit.*, Vol. I, chap. 1, and the Introduction to Pottier's Catalogue of the vases in the Louvre. See also Fowler & Wheeler's "Greek Archaeology," chap. 1.

results of the investigations that have been carried on in this fascinating field. I shall, therefore, in this paper briefly summarize the most important events in this study, and in an appendix at the end will give a list of the museums containing collections of vases.

The beginning of the study of vases was in the end of the seventeenth century. In that earliest of treatises on archæology, Montfaucon's "*L'Antiquité Expliquée*" (Paris, 1719), mention is made of them; and some are published. Previously to this, however, examples had been illustrated in the *Museum Romanum* of La Chausse, or Caussius, in 1690, and, at about the same time, by Grævius in his *Thesaurus*. In these two books we find the first appearance of any reference to the painted vases.

It may be said that works on vases can be divided into five general types, all dependent one upon the other, but all equally distinct. In the first place, there are the handbooks and treatises (in which should be included doctoral dissertations) on the history and style of Greek ceramics, and various phases of the subject; secondly, the articles on vases, in archæological or philological periodicals; thirdly, catalogues of museums or private collections, and sale catalogues; fourthly, albums or portfolios of plates, usually accompanied with an explanatory text; and lastly, reports of excavations and acquisitions. Practically all the literature on the subject falls into one of these five heads, while some books combine two or three of them.

It is the album that started the study of ceramics, and has had the longest life of any of these classes. Usually an album or portfolio is a series of plates taken from vases in different collections. It can, however, consist of plates from one collection alone. It differs then from the catalogue in not attempting to describe or portray the entire collection, as a catalogue would, but only examples selected for their artistic excellence or archæological importance.

The ancestor of all modern albums of Greek vases is the monumental work of Giovanni Baptista Passeri, called "*Picturæ Etruscorum in Vasculis*." There are three volumes, the first appearing in 1767, the second in 1770, the third in 1775. This is to this day the approved manner of publishing an album, not all at once, but different parts in different years. Passeri gives the shape of every

vase he describes, but his drawings are crude and inaccurate, there is no attempt at chronology, and most of the vases he publishes are of the Apulian style, which is late and decadent. It will be noticed that he considers them Etruscan; but at that time it was almost the universal belief, as I shall point out a little later.

The next series of albums are nearly all of private collections, and the most important of these are the albums of the Hamilton Collection, the first by D'Hancarville (1766-67), the drawings of which are quite untrustworthy, and the second by Tischbein (1791-1803) called *Vases d'Hamilton*. Tischbein's is perhaps the first accurate album to be published; but he almost invariably omits the shapes of the vases he describes, which makes it hard to use him. Furthermore, most of the Tischbein vases are inaccessible, as a large part of the collection which is portrayed by him was lost at sea. A large number of Tischbein vases passed into the famous Hope Collection, and many of them figured in the Hope Sale at Christie's in the summer of 1917.

In 1808 and 1810, A. L. Millin brought out his "*Peintures de Vases Antiques*" in two volumes, an album of vases in various collections. This was republished in a cheap form in 1891 by Salomon Reinach, who gives the various present locations of the vases there published. Millin's drawings, from the archæologist's point of view, are almost worthless. The subjects were at the time the chief features of interest to scholars. The shapes are rarely, if ever, given, and the drawings are absolutely unreliable for the study of technique. A little better was the work of F. Millingen, whose "*Ancient Unedited Monuments*" (1822-26) contained publications of some vases, but whose "*Peintures Antiques de Vases Grecs*" (Rome, 1813) is really the beginning of good work in albums. Another typical album of this period is Dubois-Maisonneuve's "*Introduction à l'Étude des Vases Antiques*" (Paris, 1817). Many albums were also made of private collections such as "*Vases de la Collection de Sir John Coghill*" by Millingen (1817), (a collection now dispersed, but several vases from which figured in the Hope Sale) which showed a great advance on his previous work. Shapes are always given, and the drawings are more accurate. Then there is Laborde's "*Vases de M. le Comte de Lamberg*" (1813-24), a

collection now also dispersed, but most of which is in Vienna; and the album of the collection of the Duc de Luynes, that most active amateur of art, which is new in Paris in the Bibliothèque Nationale (Paris, 1840).

The most important album since Passeri, however, was F. Inghirami's "*Pitture di Vasi Fittili*" (Fiesole, 1833-37; republished in 1852-56 as "*Pitture di Vasi Etruschi*"). This is usually abbreviated as V.F., and it is still an important book. Inghirami issued other portfolios as well, the most important being his "*Museo Chiusino*" as album of finds from Chiusi, the ancient Clusium. The two albums of G. Micali, "*Monumenti Inediti per Servire alla Storia degli Antichi Popoli Italiani*" (1833; usually abbreviated as "*Storia*"), and "*Monumenti Inediti*" (1844) contain vases and are of considerable importance, as is a similar album, "*Monumens Inédits*," by the Frenchman, Raoul Rochette (1828).

But the most important and far-reaching of these early albums was Stackelberg's "*Gräber der Hellenen*" (1837), made up after travelling in Greece. This book stopped the "Etruscan theory" of which I shall now speak, from growing, and proved beyond peradventure the Greek origin of the vases.

Let us now consider what progress had been made in the study of vases by means of these albums. There were up to 1827, and, indeed, in a minor degree, up to the publication of Stackelberg in 1837, two theories as to the origin, the Etruscan and the Greek. The former view was held by all the earliest authorities such as Montfaucon and Passeri; but, in 1764, the great Winckelmann brought out his "*History of Ancient Art*." In this epoch-making book, and in his "*Monumenti Antichi*," which came out in 1769, he publishes some vases, and he saw at once that their spirit was that of Greece, not Etruria; he therefore called them Italo-Greek, suggesting *Magna Græcia* as the place of their production. He was followed by most of the French scholars, such as Millin, Millingen and Laborde; but the Italians, largely through national pride, held on to the Etruscan theory as long as it was possible to do so, and Inghirami called the vases Etruscan even as late as 1856. The discovery of vases in Greece, of course, confirmed the position of the Greek protagonists.

We have seen that up to the twenties and into the thirties of the last century vases were studied almost entirely through albums. Two new features now occur, which are of importance; namely, articles in periodicals, and reports of excavations. Museums, although they had been founded back in the eighteenth century, or even earlier, had not been catalogued, nor were there catalogues of private collections, other than the sort of albums to which reference has been made, with one exception, to be recorded below.

On the anniversary of Winckelmann's birthday, December 9, 1828, an event occurred of the first importance to archæology. There was founded in Rome by a group of scholars, the Instituto di Corrispondenza Archeologica, which later became the German Archæological Institute. The inspiration that doubtless caused this, the first scientific archæological society (for the Society of the Dilettanti in England cannot be seriously compared with it) to be formed, lay in the discovery of the Etruscan necropolises of Corneto, Chiusi, Cervetri, and other sites, and the phenomenal discovery of thousands of vases in Vulci in 1828, which led to a revival of the Etruscan theory, although it was not seriously considered by the majority of scholars. The institute began at once to publish two periodicals—the *Annali dell' Istituto*, devoted to articles, and the *Bulletino dell' Istituto*, devoted to reports of excavations and acquisitions of museums. With the *Annali* came separate plates, illustrating the articles (other plates being bound with each volume) which were later bound together in groups every two or three years, and, when bound, were known as the *Monumenti Inediti dell' Istituto*.

It is at this time that one of the leading scholars of Greek vases makes his appearance, Eduard Gerhard, who is our first great name as a vase expert. He was director of the institute from its foundation till 1837, when he went to Berlin as archæologist for the museum. He recognized at once the importance of the vases from Vulci, and at first was inclined to think that there existed, in various sites in Etruria, centers for the production of vases under Greek influence. This was upheld by several other scholars, but later abandoned. Too little attention has been paid by students in general to Gerhard's excellent work, and too little credit given to him

for the advances he made in our knowledge, although his work was not as epochmaking as that of Otto Jahn, of whom I shall speak later.

Gerhard's most famous publication is his great album, published between 1840 and 1858, called "Auserlesene Griechische Vasenbilder," known usually to archæologists as A.V. Here, in 330 plates, he publishes about 350 vases, in every case giving the shape and the design as accurately as it was at that time possible to give it, with an explanatory text giving the location of each vase. It marked a great advance over any album previously published, and over the contemporary "Élite des Monuments Céramographiques" by the Frenchmen, Lenormant and De Witte. These volumes of Gerhard's are still important, and are fascinating to the archæologist, for the following reason:

Many of the vases published by Gerhard were seen by him "in the trade in Rome" and were there drawn. Of these many have since disappeared, and so we call them "lost vases." Anyone who has worked with vases long and faithfully is pretty likely to acquire a mental photograph of the more important "lost vases," which he carries around with him, aided by the actual republication of the A.V. in small line-drawings, by Reinsch, in the second volume of his "Répertoire des Vases Peints," in 1900. If I, for instance, go to a new, or an uncatalogued museum, I look instinctively for "lost vases," which are mostly taken from Gerhard. In this way it has been my fortune to find many of them, in uncatalogued museums in America and Europe.

To return to our subject. Gerhard's next most important achievement was the foundation in Berlin of a new archæological periodical, the *Archæologische Zeitung*, which lasted from 1843 till 1885. This was largely given over to vases. In the meantime, the Instituto di Corrispondenza was growing in importance, and other archæological societies were founded. In Greece, for instance, the Ἀρχαιολογικὴ Ἑταιρεία was established in 1837, and in 1846, the French School at Athens, the first archæological school in order of foundation.

Gerhard was one of the first people to adopt a system of chronology for vases. He recognized an earliest "orientalizing" class, a

black-figured, a red-figured, and a polychrome, developing from red-figured. This is the earliest attempt at a correct chronology, and, roughly speaking, these divisions are still good. There had been previous attempts at chronology, made by d'Hancarville, who, considering them Italian, dates the vases as lasting "from some centuries before the foundation of Rome" till the reign of Septimius Severus! Other attempts at chronology were made by Millingen, the Duc de Luynes and especially by Kramer⁴ and Baron De Witte, whose classification is very practical.⁵

We have now come to the greatest name of all, perhaps, that of Otto Jahn, who brought out in 1854 the first scientific catalogue to be written, that of the *Vasensammlung* of the Pinakothek in Munich. Jahn's chronology is, in the main, the same as that of Gerhard, but he falls into the same error as his contemporary in Berlin in making the dates of the Attic black-figured and red-figured styles about a century too early in each case. Although a catalogue of vases in the possession of the Elector of Brandenburg had been written as far back as 1701, nevertheless Otto Jahn's Munich catalogue is the first scientific catalogue ever to be written. It serves two purposes; for it is not only a catalogue, but the introduction which precedes the description of the vases is the first systematic handbook to be written. This introduction was for many years the standard text-book on the history and chronology of Greek ceramics; while the catalogue proper minutely describes each vase in the collection, and at the back is a series of plates, giving the shapes of the vases, with each shape numbered. Against each vase in the text of the catalogue is given the shape, according to its number in the plates. Another series of plates copies the inscriptions found on the vases. This catalogue served as a model for about thirty years. All important catalogues were written in that manner, with plates of shapes and inscriptions in the back. The ultimate development of this form of catalogue is Furtwängler's of Berlin; but the first catalogue of the British Museum, and the catalogues of Naples, Petrograd, and many other museums were of the same order.

⁴ "Der Stil und Herkunft der griechischen Vasen," Berlin, 1837.

⁵ Sale Catalogue of Durand Coll., 1836.

In 1858, an Englishman, Birch, brought out his "History of Ancient Pottery," which is the first separate handbook to be written in any language, and was for a long time the standard book. A second edition appeared in 1873. In the meantime, largely through the good work of Birch, the English periodical, *Archæologia*, the oldest of all archæological magazines, dating from 1770, began to publish important articles on vases.

We have now seen the beginnings of the systematic study of the Greek ceramographic art. The three most noteworthy developments to notice now in the modern growth of our knowledge of the subject are: (1) the discovery of the proper chronology of the vases; (2) the development of the modern illustrated scientific catalogue; and (3) the tendency towards the production of handbooks on general or special subjects connected with vases.

After Otto Jahn's catalogue, and until 1885, the interest in the study of vases grew steadily. Many catalogues were written, and many new periodicals started, which devoted much of their space to vases. The general value of archæology as a science was recognized, and archæological societies began to spring up.

The Franco-Prussian War of 1870-71 had, among other results, the effect of Germanizing the Istituto di Corrispondenza in Rome. It was one of the prices that Italy had to pay for entering Rome under Victor Emmanuel. And so this institute became generally known as the German Institute, although *Monumenti*, *Annali* and *Buletino* continued to be published in Italian just as before till 1886. In 1874, the Germans established an archæological school (called Das kaiserlich deutsche archæologische Institut) in Athens, which began in 1876 the publication of its own Mittheilungen, a quarterly periodical, which contains many articles on vases.

The year 1879 is a notable one in the history of archæology, and therefore of vases, for that year saw the birth of the two leading archæological societies of the present day—the Archæological Institute of America, which was founded by Charles Eliot Norton and others in Boston in that year, and the Society for the Promotion of Hellenic Studies, or the Hellenic Society, which was organized in London at that time. In 1880, this latter society began the publication of its semi-annual *Journal of Hellenic Studies* (J.H.S.), one of

the finest archæological magazines there is, and, at its beginning, the very finest. In 1876, the Italian Accademia dei Lincei had begun its periodical, *Notizie degli Scavi di Antichità*, a journal devoted entirely to reports of excavations. It is of interest to say in this connection that the Italians have not ceased to carry on excavations and archæological research work in spite of the war, that the *Notizie* has not in any way suspended publication, and that, in southern Etruria, especially at Cervetri, I believe, some of the finest vases have recently been found that have ever come to light. We can see then, from the indications that I have mentioned, that, up to 1885 the study of archæology was making great strides, and that, naturally enough, it was helping along the interest in vases.

In 1885, however, two events of the first importance occurred, one of them epoch-making in its significance. This makes 1885 a date to be remembered, and put with 1764 (Winckelmann), 1767 (Passeri), 1828 (foundation of the Istituto di Corrispondenza), 1837 (final confirmation of Greek theory, by the publication of Stackelberg) and 1854 (Otto Jahn's Munich catalogue) as a milestone in the road towards a full knowledge of the subject. In that year, the *Ἀρχαιολογικὴ Ἑταιρία* in Greece undertook the excavation of the Acropolis at Athens. Almost at the outset important data were found relative to the chronology of Greek vases. The fragments of pottery found in the débris which was used as filling material after the departure of the Persians in 479 B.C., and which obviously antedated the Persian invasion, contained Attic red-figured potsherds. This, of course, threw back the beginning of the red-figured technique, and also, of course the black-figured, which everyone agreed preceded it, to a much earlier date than had been supposed. This is the beginning of the working out of the true chronology of Attic vase-painting.

The year 1885 introduced other noteworthy developments as well. The Archæological Institute of America, which had founded the American School of Classical Studies in Athens, in 1881, began in this year the publication of the *American Journal of Archaeology* (A.J.A.). This periodical, a quarterly, is now recognized as one of the leading scientific archæological journals in the world. Its present editor is Dr. J. M. Paton, of Cambridge, Mass. From the

start, it has taken an interest in vases, and published many good articles.

But next to the excavation of the Acropolis, the most important event of that year was the complete Germanization of the Instituto di Corrispondenza. The *Monumenti*, *Annali* and *Bulletino* stopped publication, and the headquarters of the institute moved from Rome to Berlin. Its name was now changed to Das kaiserlich deutsche archæologische Institut, and the old building and splendid library of the Instituto became the headquarters of the German archæological school in Rome. At the same time, the German institute absorbed Gerhard's *Archæologische Zeitung*. In place of the *Annali*, there is now issued a quarterly periodical, called *Jahrbuch des K. d. archæologischen Instituts*, while the *Monumenti* has become the *Antike Denkmäler*. The *Archæologische Zeitung* has been turned into a supplement to the *Jahrbuch* called *Archæologischer Anzeiger*, devoted largely to reports of excavations, and particularly of acquisitions to museums, while the *Mittheilungen* of the Roman school has taken the place of the *Bulletino*. In all of these magazines, vases play a prominent part.

The modern illustrated scientific catalogue doubtless grew out of the sale catalogue. It is natural, when a large private collection is being sold, either at Chrystie's or the Hôtel Drouot, that the owners, or dealers acting for the owners, want to realize as large a price as they can. So that the sale catalogues early began to be rather sumptuous and to publish illustrations of the principal objects contained. Another determining factor, was, of course, the perfection of methods of photography, and the making of it cheap enough to use freely. Still, much use is made even now of drawings.

The first modern illustrated scientific museum catalogue that I knew of is Masner's of the Oesterreichisches Museum in Vienna, which appeared in 1891,⁶ and where most of the important vases are illustrated. But the best work of the nineties was done in England. The catalogues of the Ashmolean Museum in Oxford (1893) and the Fitzwilliam Museum in Cambridge (1896) are

⁶ Some steps in this direction were taken in Italy in the catalogues of the Jatta collection at Ruvo di Puglia, Italy, in 1869, and the Caputi collection in the same place in 1877, both of these catalogues being illustrated with plates of the more important unpublished vases. Both are by Signor G. Jatta.

models of what a catalogue should be, for the clearness and excellence of the text, and the beauty of the illustrations. In 1893, also, the new Catalogue of the British Museum, by Cecil Smith and Walters, began to appear, which marked an important step. In that year, too, Mr. Edward Robinson brought out his catalogue of the vases in the Museum of Fine Arts in Boston, which is now out of date, through no fault of his, but because Boston has doubled and trebled its collection since that catalogue was written.

The French have produced fine catalogues of the museums in Madrid and Athens, and especially praiseworthy is De Ridder's of the Bibliothèque Nationale in Paris: and M. Edmond Pottier, Conservateur de la Céramique Antique at the Louvre, and one of the world's leading authorities on the subject, has successfully combined catalogue and album in handling the collections in that museum, writing an unillustrated text catalogue, which brief descriptions of the different vases, and with an introduction which, when it first came out, gave the best short summary of the history of Greek pottery and of its study that had up to that time appeared, while larger volumes contain separate groups of plates, which give photographs of selected specimens, with a good account of each vase illustrated, including a complete bibliography of its previous publications, if any. The Catalogue of Athens was by Collignon in 1878; but a new edition, written in collaboration with the late Louis Couve appeared in 1902, with an atlas of plates, and a supplementary catalogue, covering accessions since that year, also with an atlas of plates, was brought out by Georges Nicole in 1912. Madrid was catalogued by the late Gabriel Leroux, one of the ablest of the younger French archæologists, who was killed at the Dardanelles.

In Italy, Pellegrini has produced, in 1900 and 1912, excellent catalogues of the collections of the Museo Civico at Bologna, but very little work has been done towards cataloguing the very rich museums of Italy, and the catalogues, where there are any, are mostly out of date, as in the case of Naples. I understand that the two leading collections in Rome, those of the Vatican and the Museo di Villa Giulia, will shortly become accessible to students by catalogues; but more important even than these is the cataloguing of

the small provincial museums, such as Chiusi, Corneto, Orvieto, Perugia and others, like Taranto in southern Italy and Syracuse in Sicily, all of which have splendid collections. Last of all, the Germans have come into the field, and a new catalogue of Munich was in progress before the war, the first volume of which, by Sieveking, made its appearance in 1912, and is a fine example of the modern illustrated scientific catalogue. The best work of the Germans, however, is in albums, of which Furtwängler and Reichhold's "Griechische Vasenmalerei," with explanatory text, continued by Hauser after Furtwängler's death, in 1907, is indispensable to any worker with vases, and a magnificent piece of work, while Riezler's "Weissgrundige Attische Lekythen," combining handbook and album, is also a very useful work.

But the genius of the present day lies toward handbooks, in which either the whole field, or parts of it, are studied and discussed. The Germans, with their minute plodding, and absolutely uninspired thoroughness, have produced handbooks for the most part on small sections of the field such as inscriptions on vases, signatures, dedicatory inscriptions or *καλός*-names, and the like; very useful books, but for the most part of no literary merit, although the scientific archæologist must know them from cover to cover. Of these books, the most important is Paul Hartwig's "Die griechischen Meisterschalen des strengen rothfigurigen Stils," which has a text and an atlas of plates, and is invaluable for the study of technique.

England has given us, in H. B. Walter's "History of Ancient Pottery" (London, 1905), a reworking of Birch's out-of-date handbook, which is, even today, the standard text-book on Greek vases, not even superseded, in my opinion, by Perrot's "La Céramique D'Athènes" (Vol. X. of Perrot and Chipiez's "Histoire de l'Art dans l'Antiquité") which appeared in 1914, just before the lamented death of its author, and which is a very important book. But Walters remains the standard text, although there are many imperfect books, which is, even today, the standard text-book on Greek vases, in the years since it appeared. England has also produced probably the most inspired worker in vases alive today, though perhaps not as universal in his knowledge as some of the workers in France,

Germany or the United States, in Lieutenant J. D. Beazley, of Christ Church, Oxford.⁷ Before the war, Lieutenant Beazley had produced, principally in the *Journal of Hellenic Studies*, but also in other periodicals, a series of articles, little short of masterly, on the technique of Attic red-figured vases. He discovered a series of previously unknown vase-painters, and, so great was his knowledge of the museums of the world, that he was able to lay his finger on almost every extant vase by their hands. Since the war, some articles by him have appeared, but I understand that he is now (1918) engaged in war-work at the Admiralty, and naturally has no time for archaeological study. A book by him on vases in America will shortly appear.

In France, besides Perrot's book already referred to, Pottier has written a charming monograph, "Douris et les Peintres de Vases Grecs" (English translation by Miss Bettina Kahnweiler) in a popular style in the little series called "Les Grands Artistes." Collignon, the author of the Athens catalogues, in collaboration with the late O. Rayet, wrote a "Histoire de la Céramique Grecque" (Paris, 1888) which for nearly twenty years was the standard text on the subject, being only superseded by Walters. But the best work and the most useful that the French have done is that of M. Salomon Reinach, who has republished, in a form accessible to students, and very cheap, in two volumes, called "Répertoire des Vases Peints Grecs et Etrusques" (Paris, 1898 and 1900) a number of unusual and rare publications. In the first volume, he republishes the St. Petersburg "Comptes-Rendus" (an unwieldy and rare album), the plates of vases from the *Monumenti*, *Annali*, and *Archaeologische Zeitung*, also plates of vases from the defunct Italian periodicals *Bulletino Archeologico Napolitano*, *Bulletino Italiano*, and *Museo Italiano di Antichità Classica*, and the early plates of vases in the *Ἑφημερίς Ἀρχαιολογική*, the organ of the *Ἀρχαιολογικὴ Ἑταιρεία*. In the second volume he republishes Millingen's *Vases de Coghill*, Gerhard's *A.V.*, the albums of Laborde (*Vases de Lamberg*), the Duc de Luynes, and Tischbein (*Vases d'Hamilton*), and an album by Roulez of selected vases in the Museum in Leyden.

⁷ Since writing this I learn that Lieutenant Beazley has been promoted to captain.

In an earlier volume (Paris, 1891) he had republished the albums of Millin and Millingen. In every case, where known, he gives the present location of each vase he publishes. At the back of the "Répertoire," there is a splendid bibliography, which is brought up to date later by Walters.

American scholars have taken very kindly to vases, and the best short chapter on vases and their history and chronology ever written, is that by the late Professor J. R. Wheeler of Columbia, in Fowler and Wheeler's "Greek Archæology" (New York, 1909). Other names of good men and women who work in this field are Paul Baur of Yale, George H. Chase of Harvard, D. M. Robinson of Johns Hopkins, and especially J. C. Hoppin of Bryn Mawr, whose "Euthymides and his Fellows" has recently been published by the Harvard University Press, and is a very important book; Edward Robinson, director of the Metropolitan Museum in New York, who when connected with the Museum of Fine Arts in Boston, wrote the catalogue of their vases; and Arthur Fairbanks, director of the Museum of Fine Arts in Boston, who has written the standard book on that class of vases known as Attic White Lekythoi, and whose catalogue of the Boston vases is impatiently awaited. Among women, there is Miss Hetty Goldman of New York, who has written some excellent articles; Miss Gisela M. A. Richter of the Metropolitan Museum in New York, whose work is of the highest order; and Miss Mary Hamilton Swindler of Bryn Mawr, who published so ably the fine red-figured cylix owned by this Society, and who has published a number of most praiseworthy papers in the *American Journal of Archæology*.

The twelve great museums of the world, for vases as I would rank them, are: (1) The British Museum, (2) the Antiquarium, Berlin, (3) the Musée du Louvre, Paris, (4) the Museo Nazionale, Naples, (5) the National Museum, Athens, (6) the Alte Pinakothek, Munich, (7) the Museum of Fine Arts, Boston, (8) the Hermitage, Petrograd, (9) the Etruscan Museum of the Vatican, (10) the Metropolitan Museum, New York, (11) the Museo Civico, Bologna, (12) the Bibliothèque Nationale, Paris.

Thus one sees that this country possesses two collections of vases of the first rank.

A list of the museums of the world that contain collections of Greek vases will follow this article. Important museums are printed in italics.

MUSEUMS CONTAINING COLLECTIONS OF VASES.

ENGLAND.

London; *British Museum*. (Catalogue by C. Smith and Walters, in progress, all but Vol. I., part 1, being out. Vol. I., part 2, appeared in 1912; Vol. II. in 1893; Vol. III. in 1896; Vol. IV. in 1896.)

Victoria and Albert Museum. Uncatalogued.

Soane Museum. Uncatalogued.

Oxford; *Ashmolean Museum*. Catalogue by P. Gardner (1893).

Cambridge; *Fitzwilliam Museum*. Catalogue by E. A. Gardner (1896).

Deepdene; *Hope Collection*. Dispersed at a Public Sale at Christie's in 1917. Sale Catalogue published in that year. A scientific catalogue by E. M. W. Tillyard is in preparation.

Edinburgh. Museum.

Harrow-on-the-Hill; Harrow School Museum Catalogue by C. Torr (1887).

Castle Ashby; Nothampton Collection.

Richmond; Cook Collection.

FRANCE.

Paris; *Musée du Louvre*. Catalogue by E. Pottier (in progress).

Bibliothèque Nationale. Catalogue by A. de Ridder (1902).

Petit Palais. Dutuit Collection. Album, but no catalogue.

Musée des Arts Decoratifs.

Musée Guimet.

Boulogne-sur-Mer; *Musée Municipal*. Guide by H. E. Sauvage (1898). See also E. Pottier in "Album Archéologique des Musées de Province" (Paris, 1890-1891; pp. 68-101).

Compiègne; Musée Vivenel. A catalogue (rare) exists.

Rouen; Museum.

Toulouse; Museum. Catalogue by Roschach, 1892.

Lyons; Museum.

Sevres; Museum.

Marseilles; Museum. Catalogue by Froehner (1897).

Amiens; Musée de Picardie.

Abbeville; Museum.

Beziers; Museum.

Nearly all the French provincial museums have small collections of vases.

BELGIUM.

Brussels; Musée du Cinquantenaire. Catalogue (of Ravestein Collection) by Ravestein (1884).

GERMANY.

Berlin; *Antiquarium*. Catalogue by Furtwängler (1885). See also files of the *Archaeologischer Anzeiger*, for accessions since that year.

Munich; *Pinakothek*. Catalogue by Otto Jahn (1854). The first volume of a new Catalogue by Sieveking (1912) has appeared.

Würzburg; *Antikenkabinet*. Catalogue by Urlichs (1869-72).

Altenburg; Museum.

Bonn; Museum of the University. Description by Kekule.

Breslau; Museum. Catalogue by Rossbach (1899).

Brunswick; Museum.

Dresden; *Antikensammlung*. Catalogue by Hettner (1881). See also files of the *Archaeologischer Anzeiger*, as for all German Museums.

Frankfurt-am-Main; Städels-Institut.

Gotha; Museum.

Göttingen; Museum of the University. Description by Jacobsthal (1913).

Hamburg; Museum für Kunst und Gewerbe. Description by Ballheimer (1905).

Heidelberg; Museum of the University.

Karlsruhe; Museum. Catalogue by Winnefeld (1887).

Cassell; Museum.

Hanover; Kestner Museum.

Jena; Museum of the University.

Leipzig; Museum.

Hauser Collection.

Strassburg; Museum.

Schwerin; Museum.

Weimar; Museum.

Munich; Loeb Collection.

Würzburg; Banko Collection.

AUSTRIA.

Vienna; *Oesterreichisches Museum*. Catalogue by Masner (1891).

Kunsthistorisches Museum. (Formerly Antikenkabinet.) Catalogue by Sacken und Kenner. See also Laborde's *Vases de Lamberg*.

University.

Cracow; Museum. See De Witte, *Catalogue de la Collection a l'Hôtel Lambert*, most of which went to Cracow.

Czartoryski Collection.

Prague; Pollak Collection.

Trieste; Museum.

Sarajevo; *Bosnisch-herzegovinisches Landesmuseum*. Catalogue by Bulanda (1912).

ITALY.

Bologna; *Museo Civico*. Catalogues by Pellegrini (1900 and 1912).

Corneto; *Museo Etrusco Tarquiniese*.

Florence; *Archaeological Museum*. Description by Milani (1913).

Naples; *Museo Nazionale*. Catalogue by Heydemann (1872), out of date, but no other exists.

Ruvo di Puglia; *Jatta collection*. Catalogue by G. Jatta (1869).

Caputi Collection. Catalogue by G. Jatta (1877).

Rome; *Museo Etrusco al Vaticano*. Catalogue in preparation. See also the album called "*Museo Gregoriano*" (Rome, 1842).

Museo di Villa Giulia. Catalogue in preparation. See *Monumenti Antichi dei Lincei*, vols. XIV., pp. 269-308, and XXIV., pp. 345-400.

Conservatori Palace. Before the war, a catalogue was contemplated by students of the British School at Rome.

Torlonia Collection.

Castellani Collection.

Hartwig Collection.

Syracuse; *Archæological Museum*. See Mon. Ant., Vol. XVII.

Taranto; *Archæological Museum*.

Adria; Museo Bocchi. Description by Schöne (1874).

Arezzo; Museum.

Capua; Museo Campana. Catalogue by Patroni.

Bari; Archæological Museum.

Chiusi; Museo Etrusco.

Girgenti; Archæological Museum.

Catania; Archæological Museum.

Biscari Collection.

Milan; Museo Poldi-Pezzoli.

Orvieto; Museo Civico.

Faina Collection. Catalogue by Cardella (1888).

Palermo; Museo Nazionale.

Parma; Museum.

Perugia; Museo Etrusco.

Turin; Museo dell' Università. Description by Fabretti (1872).

Verona; Museum.

Other small museums, collections, etc., in Sicily and Sardinia:

Cagliari; Museum.

Caltanissetta; Museum.

Castrogiovanni; Museum.

Noto; Museum.

Terranuova (Gela); various private collections.

Catania; various private collections.

Girgenti; various private collections.

SWITZERLAND.

Zürich; Museum of the University. Catalogue by Blümner.

Geneva; Palais d' Ariana.

Berne; Historical Museum.

RUSSIA.*

Petrograd; *Hermitage*. Catalogue by Stephani (1869).

Academy.

Stroganoff Collection(?).

Pisareff Collection(?).

Moscow; Museum.

Dorpat; Museum of the University.

Odessa; Museum.

Kertsch; Museum.

Nowikow Collection.

Kiev; Museum.

SPAIN AND PORTUGAL.

Madrid; *Archæological Museum*. Catalogue by Leroux (1912).

Barcelona; Museum.

Lisbon; Museum.

HOLLAND.

Leyden; *Rijksmuseum*. Catalogue by Holwerda (1905). See also
Roulez, *Choix de Vases Points du Musée de Leyde*.

Amsterdam; Six Collection.

The Hague; Scheurleer Collection. Catalogue (The Hague, 1909).

DENMARK, SWEDEN.

Copenhagen; Thorwaldsen Museum. Catalogue by Birket Smith
(1862).

Stockholm; Museum.

GREECE.

Athens; *National Museum*. Catalogue by Collignon and Couve
(1902) and a supplementary catalogue by Nicole (1912).

Acropolis Museum. Catalogue in progress by Botho Graef.

Various private collections.

Peiræus; Museum.

Eleusis; Museum.

Thebes; Museum.

* What conditions exist in Russia at present it is impossible to state.
This is the ante-bellum condition.

Nauplia; Museum.

Myconos; Museum.

Delos; Museum. Impossible to take notes in this Museum.

ASIA MINOR, CYPRUS, AND EGYPT.

Smyrna; various private collections.

Nicosia; Cyprus Museum. Catalogue by Myres and Richter (1899).

Various private collections at various places on the Island of Cyprus.

Cairo; Museum. Catalogue by Edgar (1913).

Malta; Valetta Museum.

UNITED STATES.

Boston; *Museum of Fine Arts*. Catalogue by E. Robinson (1893), out of date. A new Catalogue has been promised.

New York; *Metropolitan Museum of Art*. Handbook by Miss G. M. A. Richter (1917).

Philadelphia; University Museum.

Memorial Hall.

Cambridge; Fogg Art Museum.

Collection of Classical Department, Harvard University.

New Haven; Yale University.

Baltimore; Johns Hopkins University.

Walters Collection.

Princeton, N. J.; Art Museum of Princeton University.

Worcester, Mass.; Art Museum.

Chicago; Art Institute.

Field-Columbian Museum.

St. Louis; Art Museum.

Stanford University, Cal.; Collection of Classical Department.

Brunswick, Me.; Walker Art Gallery, Bowdoin College.

Washington; National Museum.

AUSTRALIA AND NEW ZEALAND.

Sydney; Nicholson Museum, University of Sydney. Catalogue by Louisa Macdonald (1898).

Auckland, N. Z.; Museum.

OBITUARY NOTICES
OF MEMBERS DECEASED.

OBITUARY NOTICES OF MEMBERS DECEASED.

AMOS PEASLEE BROWN.

(Read January 4, 1918.)

As we look over the roll of men who have devoted their lives to any special line of research, we find represented there a wide range of character and temperament. Some have courted publicity, others from the sheer force of their personality, or from the nature of their achievements, have been constantly in the public eye, while others again, averse to notoriety, have quietly and unostentatiously pursued their studies, content with the acquirement of knowledge for its own sake, and from excessive modesty, refraining from publishing to the world much that would have been widely welcomed. This latter group never receive the recognition to which their qualifications would entitle them, and their true worth is known only to the few to whom is given the privilege of close association with them. To this class belonged the subject of the present sketch—well known, it is true, as a geologist, a mineralogist, and a teacher, but possessed of a breadth of knowledge little suspected, except by those few who knew him in the intimacy of close friendship, and which is only partially reflected in the publications which he has given to the world.

Amos Peaslee Brown was born in Germantown, Philadelphia, on December 3, 1864, the son of Amos Peaslee and Frances Brown and the fourth child of a family of seven sons and two daughters. His parents were cousins, his paternal grandfather, also Amos Peaslee, had settled in Maryland, where he was engaged in agriculture, while his grandfather on his mother's side, Jeremiah Brown, with two other brothers, Moses Brown and David S. Brown, had established themselves in Philadelphia as dry-goods commission merchants, founding one of the first business houses of this sort in the city. The ancestor of the family in America was Henry Brown,

who in 1639 had emigrated from England to Haverhill, Massachusetts, and who became one of the early settlers of Salisbury in the same state.

Jeremiah Brown married Elizabeth Stewardson, sister of Dr. Thomas Stewardson, a well-known medical practitioner of Philadelphia and a man of broad scientific knowledge, a member of the Academy of Natural Sciences and a botanist of considerable standing. If we seek for the origin, in past generations, of the love of science so strongly marked in Dr. Amos Brown, we shall probably find it traceable to the Stewardsons.

Brown's earliest education was received at a small private school, but in the autumn of 1877 he entered the Germantown Academy, which had that year been placed in charge of a new and deservedly popular principal, Dr. William Kershaw.

At school Amos Brown was always at the head of his class. He was one of those fortunate boys who seem able to master their studies with very little effort, and was always especially proficient in mathematics. At the close of his second year he received the phenomenal average of 100 in each of the subjects in which the class was examined. Deciding to take a scientific course in college he did not study Greek and dropped Latin in his last years at school. He was thus able to combine two years' work in one and graduated in June, 1882, entering the University of Pennsylvania in the following autumn.

He took the Towne Scientific Course, specializing in mining engineering after the sophomore year and graduated in June, 1886.

He remained at the university another year, pursuing his studies in the post-graduate course in mining, and received his degree of E.M. in June, 1887.

Soon after graduation Brown secured a position as aide on the Second Geological Survey of Pennsylvania, under the late Charles A. Ashburner, then assistant geologist of the survey, and also assistant on the United States Geological Survey, in charge of coal statistics.

He worked here in the bituminous region until June 18, 1888, when he returned to Philadelphia and accepted a position under Mr. Benjamin Smith Lyman, who had undertaken a survey of the New

Boston and Morea coal lands in Schuylkill County, near Pottsville. The survey was a private enterprise, but the map was afterward published by the State Geological Survey. This work kept Brown in the field until late in the autumn, while the actual drawing of the map was done in Philadelphia in the winter. In the following spring Mr. Lyman engaged in a survey and report on the "New Red" formation of Bucks and Montgomery counties, in which Brown again acted as his assistant and prepared an account of the igneous rocks of the district, which accompanies Mr. Lyman's report. His name appears on both the Bucks County map and that of the Morea anthracite district as first assistant. In the early autumn of 1889, before the Bucks County survey was completed, Brown left Mr. Lyman to accept a position as instructor in mining at the University of Pennsylvania, under his old professor, Dr. Koenig, and here he remained for practically the rest of his life. In 1890 he was instructor in mining and metallurgy; in 1892 professor of mineralogy and geology in the auxiliary department of medicine, which he held until the abolishment of the department in 1898. On March 5, 1895, he became assistant professor of mineralogy and geology in the college faculty, and full professor in the spring of 1903, a position which he continued to hold until the spring of 1917, when he was forced to resign on account of failing health. From the autumn of 1892, after Dr. Koenig's retirement from the University, Brown took over the entire direction of the department, teaching in all branches of the subject—mineralogy, geology, lithology, crystallography, mining and metallurgy. Soon after his return to the university he began studying for the degree of Doctor of Philosophy, which was conferred upon him at the commencement on June 16, 1893.

While not at all averse to field work, Brown's duties at the University were exceedingly congenial. He liked teaching, and the association with other scientific men was very enjoyable, while, established at his home once more, he was able to pursue his various researches to his heart's content.

After he returned to Philadelphia, Brown became a frequent visitor to the Academy of Natural Sciences, and on January 27, 1891, he became a member. For several years he was one of the most

regular attendants at the weekly meetings. He joined the Microscopical and Biological Section of the Academy, where he was distinctly in his element. The association with men who were devoted to this, his favorite study, he enjoyed to the utmost; while they found in him a man remarkably well informed upon the whole field of microscopical research. At the beginning of 1892 he was chosen director of the section, a post which he held for two years. He later became a member of the committee on the award of the Hayden Medal serving until his death, while in 1897 and again from 1900 to 1905 he delivered the lectures on geology and mineralogy in the Ludwick Free Courses at the Academy.

During the time of his first activity at the Academy of Natural Sciences, he became closely associated with Edward D. Cope, who was then professor of mineralogy and geology—later of zoology and comparative anatomy—at the University of Pennsylvania, and who thoroughly appreciated Brown's ability and broad knowledge. In the summer of 1893, having arranged for an exploration of some of the fossil beds of the west in the interests of the Academy, Cope invited Brown to become his associate on the trip, an invitation which he eagerly accepted. Their explorations began at Bismarck, N. D., on July 10, and covered parts of both North and South Dakota, the Cimmaron River District of Oklahoma, the northeastern border of the Staked Plains of Texas and portions of Kansas, coming to a close on September 4, at Galena, Mo. Cope paid especial attention to the fossil vertebrates, while Brown devoted himself to the invertebrates. The results of the reconnaissance are set forth in a paper by Cope in the *Proceedings* of the Academy,¹ in which will be found several notes credited to Brown.

Up to this time Brown had enjoyed excellent health. He possessed an iron constitution and had therefore never found it necessary to exercise any care whatever in the matter of exposure or overwork. Now, however, possibly from overtaxing his strength on the western trip, he suffered a severe attack of illness, followed in 1895 by another similar attack. This made him very cautious about exposing himself and he seldom went out at night, giving up

¹ "Observations on the Geology of Adjacent Parts of Oklahoma and N. W. Texas," *Proc. Acad. Nat. Sci. Phila.*, 1894, pp. 63-68.

almost entirely the evening meetings at the Academy, and not until 1901 did he again take part to any extent in the scientific activities of the city, except in connection with his duties at the University.

On May 17 of that year he was chosen a member of the American Philosophical Society and at once became interested in its meetings, as he had been in those of the Academy ten years before. He served on several of the committees and on January 3, 1908, was elected one of the secretaries, an office which he continued to hold until his death. He was a regular attendant at the meetings, except when prevented by failing health, and was a painstaking, faithful and loyal officer. He joined several other societies, but took no active part in their proceedings. He was elected a member of the American Institute of Mining Engineers on February 24, 1888; a member of the Franklin Institute in April, 1890; a member of the American Association for the Advancement of Science in 1901, and a fellow in 1906; a fellow of the Geological Society of America on December 27, 1905, and a member of the American Museum of Natural History in December, 1916. He was also a charter member of the Pennsylvania Chapter of the Society of the Sigma Xi and a trustee of his old school, the Germantown Academy.

In August, 1902, he took a cruise along Labrador coast, and camped for several weeks at Dove Point, at the head of Sandwich Bay. He made a valuable collection of the flowering plants of the region for the Academy's herbarium but devoted his attention mainly to geological problems and to a study of the general geology and topography of the country, and the grosser features of the fauna and flora. He had the faculty of storing away such general observations, made on his various trips, and holding them at his command for immediate use in future discussions or comparisons. In 1904 he made a reconnaissance of the central Rocky Mountains for the purpose of investigating certain mining properties and in the succeeding years made one or more similar trips to Utah, Nevada and Oregon, continuing on to San Francisco on one occasion, where he investigated with intense interest the effects of the great earthquake.

Up to 1900 Amos Brown had published comparatively little. There was an early boyhood paper on the tiger beetles, published

anonymously in an amateur journal,² and in 1888 an admirable account of the "Modes of Occurrence of Pyrite in Bituminous Coal,"³ prepared while engaged on the State Survey. In this he recognized five forms of occurrence and traced the origin of the pyrite to the iron content of decomposing plants affected by the sulphur from gypsum or hydrogen sulphide. Nodular pyrite he suggested was formed from fish remains in the same way; while attention is called to the present-day formation of pyrite in the scum seen on stagnant pools. In 1894 he published "A Comparative Study of the Chemical Behavior of Pyrite and Marcasite,"⁴ which was his thesis for the degree of Doctor of Philosophy. This is distinctly a piece of chemical research, dealing with the relative oxidation of sulphur in these two mineral forms of FeS_2 , by various solutions, as well as the solubility of the iron in various acids. There were two short papers⁵ in 1891 and 1892 in which the early spiral form of *Baculites* is described for the first time, the former of which was reprinted in scientific journals both of this country⁶ and in London.⁷ He published the first definite account of the crystallization of molybdenite in 1896⁸ and in 1898 a scholarly account⁹ of "Jade and Other Green Stones," which was a summary of a lecture given at the Museum of Science and Art of the University of Pennsylvania. There were several short notes on microscopical¹⁰ and geological¹¹ subjects published in 1896 and 1897 and the notes in Lyman's report¹² and in Cope's paper¹³ already referred to. In 1901 he also brought out a new edition of Erni's well-known textbook, "Mineralogy Simpli-

² *The Amateur Naturalist*, III., No. 1.

³ *Trans. Amer. Inst. Mining Eng.*, 1888, pp. 539-546.

⁴ *Proc. Amer. Philos. Soc.*, XXXIII., 1894, 225-243.

⁵ *Proc. Acad. Nat. Sci. Phila.*, 1891, pp. 159-160, and 1892, pp. 136-141.

⁶ *The Nautilus*, V., 1891-1892, pp. 19-21.

⁷ *The Geological Magazine* (London), July, 1891.

⁸ *Proc. Acad. Nat. Sci. Phila.*, 1896, pp. 210-211.

⁹ *Bull. Mus. Sci. and Art*, Univ. of Penn., I., No. 3, pp. 140-145, April, 1898.

¹⁰ "Bog Moss Leaves," *Amer. Monthly Microscop. Jour.*, XVIII., 1897, 232.

¹¹ "Red Color of Certain Formations," *Amer. Geologist*, XVII., 1896, p. 262. "Section of Chalcedony," *Amer. Monthly Microscop. Jour.*, XVIII., 1897, pp. 235-235.

¹² "Report on the New Red of Bucks and Montgomery Counties," Final Rept. Penna. State Geological Survey, Vol. III., Pt. II., pp. 2589-2638, 1895.

¹³ *Proc. Acad. Nat. Sci. Phila.*, 1894, pp. 63-68.

fied,"¹⁴ which was used by his classes at the University. Part II. of this work was entirely rewritten, while Part III., on "Physical Determinative Mineralogy," was wholly original and reflects Brown's views on the importance of sight identification of minerals.

In 1904 Brown began work upon what was to prove his greatest contribution to science,¹⁵ a piece of research, the far-reaching importance of which has perhaps not even yet been fully appreciated. Dr. Edward T. Reichert, professor of physiology in the medical department of the University of Pennsylvania, had begun in 1902 some investigations as to the differentiation and specificity of corresponding proteins and other vital substances in relation to biological classification and organic evolution. He had come to the conclusion that the hemoglobins of animals offered excellent possibilities in this line of investigation and also that their characters could best be compared and their relationships ascertained through a study of their crystallography. "Not being an authority in the science of crystallography," wrote Dr. Reichert, "I associated with me in 1904, one of my colleagues, Professor Amos Peaslee Brown, upon whom has fallen that portion of the work which demanded the services of an expert crystallographer." The enormous amount of work that Brown contributed to the undertaking can thus be readily appreciated by anyone who consults the portly volume, embodying the results of the investigation, which was issued in 1909 by the Carnegie Institution of Washington, under whose grant the prosecution of the work was made possible. Several preliminary reports on the progress of their work were issued by Professors Reichert and Brown,¹⁶ one of which was presented at the general meeting of the American Philosophical Society, in the spring of 1908. The hemoglobin investigation involved the crystallization and

¹⁴ "Mineralogy Simplified." Third edition, Philadelphia, Henry Carey Baird & Co.; London, Sampson Low, Marston Co., Ltd., pp. i-xxvii + 1-383, 1901. (Fourth edition of the same with further additions was issued in 1908.)

¹⁵ "The Crystallography of Hemoglobins," by Edward Tyson Reichert, M.D., and Amos Peaslee Brown, Ph.D., Carnegie Institution of Washington, No. 116, 4to, pp. i-xviii + 1-338, with 100 plates, 1909.

¹⁶ Yearbook of the Carnegie Institution for 1907, p. 218 (1908). *Proc. Soc. Biology and Medicine*, 1907-1908, V., p. 66. *Proc. Amer. Philos. Soc.*, XLVII., 1908, pp. 298-301.

examination of hemoglobin from the blood of over one hundred species of animals and the preparation of 2,500 photomicrographs, 600 of which appear in the report along with upwards of 400 outline drawings. Briefly the investigation shows that the crystals from the several species of a genus all belong to one crystallographic group—those of the cats (Genus *Felis*) for instance, being isomorphous just as strictly as are the rhombohedral carbonates among minerals. Specific characters are also evident in the differences in the angles of the crystals. The importance of such facts in considering the relationship of species and genera and in the whole field of phylogeny will readily be appreciated. An able review of the work has been published by Dr. Leo Loeb¹⁷ from which one can obtain a good estimate of the value of the conclusions reached by the authors, from the standpoint of the biologist. In his review Professor Loeb also quotes opinions of several expert crystallographers, on this phase of the investigation. From these we may quote the statement of Professor Edward H. Kraus, of the University of Michigan, that: "From the crystallographic standpoint Professor A. P. Brown has done a remarkable piece of work which is deserving of the highest credit," and that of Dr. J. E. Pogue, of the Smithsonian Institution, who says: "The actual crystallographic and optical details are apparently determined with skill and accuracy. The photomicrographs are excellent and the line drawings good."

The constant application incident to this protracted piece of research and the severe strain which it entailed were too much for Brown, and in the summer of 1909 he suffered a severe nervous breakdown, which necessitated a complete rest from his duties at the University, during the next college year.

He took a trip to Jamaica in February, 1910, his first experience in the tropics, and became so much interested in the natural history of the island that he returned for another visit in April, passing on this time to Panama, where he studied the geological formations exposed in the canal cuts and discovered some interesting beds of fossils from which he made valuable collections. The study of these upon his return to Philadelphia showed them to be of such

¹⁷ *Science*, XXXIII., pp. 147-150, January 27, 1911.

importance that he was led to make still another trip in August for the purpose of securing additional material.

Brown brought his collections to the Academy of Natural Sciences, and with the assistance of Dr. Henry A. Pilsbry, the noted malacologist, began to work them up for publication. For the next three years a large part of his spare time was spent in Dr. Pilsbry's quarters at the museum. The latter, being actively engaged in publication, stimulated Brown to prepare many papers which would probably never have appeared had he been left entirely to himself, since he was always skeptical as to the importance of his researches and the advisability of publishing the results. In several instances Dr. Pilsbry gave him the benefit of his vast knowledge of the mollusca, in working up the systematic portion of the reports, and they were published under their joint authorship.

Thanks to Dr. Pilsbry's advice and stimulation Brown published more papers during this period than in all the rest of his career. As joint authors they prepared in 1911 a paper on "The Fauna of the Gatun Formation, Isthmus of Panama,"¹⁸ based upon Brown's collections of the previous year. In the introduction he explains that the study of the specimens fully bore out his impression, formed during a hasty reconnaissance of the exposures along the Canal and railway, that the several shell-bearing formations which have been given distinctive names really all belong to one stratigraphic unit. He and Dr. Pilsbry moreover agree that this is more likely to prove to be Oligocene than Eocene, as Dall has regarded it, and call attention to its resemblance to the Santo Domingo beds studied by Gabb. Thirty-seven new species were described in this paper, while thirty-three more were named in two supplementary publications,¹⁹ based upon material obtained by Professor W. B. Scott, in 1911. Brown was also associated with Dr. Pilsbry in a report on a collection of fossils from Wilmington, N. C.,²⁰ which was received at the Academy about this time, while he published independently an ac-

¹⁸ "Fauna of the Gatun Formation, Isthmus of Panama," *Proc. Acad. Nat. Sci. Phila.*, 1911, pp. 336-373.

¹⁹ "Fauna of the Gatun Formation, Isthmus of Panama," II., *Proc. Acad. Nat. Sci. Phila.*, 1912, pp. 500-519. "Two Collections of Pleistocene Fossils from the Isthmus of Panama," *ibid.*, 1913, pp. 493-500.

²⁰ "Notes on a Collection of Fossils from Wilmington," *ibid.*, 1912, pp. 152-153.

count²¹ of some new Cycads and Conifers which were sent to the museum from the "New Red" formation of Bucks County, Pa., a region with which he had become very familiar during his association with Mr. Benjamin Smith Lyman, on the State Survey.

Another important paper was prepared from data collected on his Labrador trip nine years before, entitled, "The Formation of Ripple Marks, Tracks and Trails."²² He had found that the broad clay and sand flats of Sandwich Bay, Labrador, which were covered by shallow water at high tide, exhibited wonderful series of ripple marks which bore a striking resemblance to those seen in the Triassic rocks. He immediately began a minute study of the water action in order to ascertain just how they were formed, and discovered that they were of two kinds—caused respectively by deposit and erosion. The many tracks and marks on these clay beds were also carefully studied and many of them proved practically identical with certain tracks and trails in the Connecticut Trias described by Hitchcock as those of annelids, fishes, etc., to which he had given distinctive names on the basis of these tracks. Brown found that a pebble to which a large sea-weed (*Ulva*) was attached made a perfect "annelid" trail, the sea-weed buoying it up and allowing it to drag slowly along on the bottom. Pieces of other sea-weeds and bits of spruce boughs rolled along by the water produced other tracks, some of which were counterparts of those described as belonging to a supposed jumping animal called "*Saltator*," while the bifid and trifid fruiting tips of Furoid sea-weeds made tracks strikingly like those of certain small reptiles. This paper is an excellent example of the clearness of Brown's observation and the activity of his reasoning powers.

On the Jamaica trips the large land mollusks had attracted his special attention and his first paper on this material dealt with variation in certain species of *Pleurodonte*.²³ He had made intensive studies of various colonies of each of several species and endeavored

²¹ "New Cycads and Conifers from the Trias of Pennsylvania," *ibid.*, 1911, pp. 17-21.

²² "The Formation of Ripple Marks, Tracks and Trails," *ibid.*, 1911 pp. 536-547.

²³ "Variation in Some Jamaican Species of *Pleurodonte*," *Proc. Acad. Nat. Sci. Phila.*, 1911, pp. 117-164.

to correlate the variations which they exhibited with differences of environment, and to show the effect of isolation in their evolution. To illustrate graphically the extent of their variation he devised some ingenious plottings and curves, based upon actual measurements of each individual shell, for by adopting measurements as his basis of comparison he hoped to eliminate as far as possible the personal equation. This whole investigation illustrated the constant trend of his mind toward mathematical methods. Another paper along very similar lines dealt with variation in two species of *Lucidella*.²⁴ Still another Jamaican study was responsible for a paper on the method of locomotion in certain land snails²⁵—a distinctly original piece of work. He had found that certain species possessed a comparatively very rapid rate of progression and a careful study demonstrated that they had an entirely different method of locomotion from that of the majority of snails. The foot, he found, touched the surface upon which they walked only along its edges, while the wave motions which traversed it were in the opposite direction to that usually prevailing in these mollusks. Furthermore the shell was carefully balanced on the operculum and swayed from side to side as the animal advanced. The rapidity of the wave motions and the exact rate of progress were worked out in much detail.

During the period just described two mineralogical publications were issued in which Brown's name appears as joint author. One of these, in the preparation of which he was associated with Dr. Persifor Frazer, consisted of a series of tables for the determination of minerals by physical properties,²⁶ while the other in which Dr. Frederick Ehrenfelt was his associate was a report on the minerals of Pennsylvania²⁷ published by the Topographical and Geological Survey of the State in 1913.

In the summer of 1913 Brown made another trip to the tropics, touching at Georgetown, British Guiana, and spending some time

²⁴ "Variation in Two Species of *Lucidella* from Jamaica," *ibid.*, 1913. pp. 3-21.

²⁵ "The Method of Progression of Some Land Operculates from Jamaica," *The Nautilus*, XXIV., No. 8, December, 1910, pp. 85-90.

²⁶ "Tables for the Determination of Minerals by Physical Properties," Philadelphia, J. B. Lippincott & Co., 1910, pp. i-xiii, I., 1-125.

²⁷ "Minerals of Pennsylvania," Topog. and Geolog. Survey of Penna. Report No. 9, pp. 1-160, 1913.

on the island of Antigua. Here he made a representative collection of fossils and on his return published a comprehensive account of the geology of the island,²⁸ reviewing the literature of the subject and describing his own collection, while in the following year in conjunction with Dr. Pilsbry he published a short paper on the fresh-water mollusca of the Antiguan Oligocene.²⁹ In these contributions eleven new forms are described. His last publication,³⁰ also in conjunction with Dr. Pilsbry, dealt with collections of Oligocene fossils from Cartagena, Colombia and Haiti, collected by Mr. Lloyd B. Smith. Twenty-one new species and subspecies were here described.

While Dr. Brown's trips to the tropics were distinctly beneficial and he was able to return to his classroom, nevertheless his recovery was only partial. In 1911 and 1912, moreover, he was twice operated upon for gallstones, an additional strain on his weakened constitution, and during the past two or three years he seemed to have little ambition to engage in any serious scientific research. In spare moments, however, in the seclusion of his home, he continued his microscopical studies, now as ever his chief diversion.

Another nervous breakdown at the close of 1916 was followed in the spring by a partial paralysis which compelled him to definitely resign his professorship at the University of Pennsylvania, where he had now been engaged in teaching for over twenty-seven years. In the autumn his condition was further complicated by the development of a severe carbuncle, which his weakened system was powerless to combat, and he passed away on October 9, 1917, at Atlantic City, N. J., where he had been taken in the hope that the change of air and surroundings might prove beneficial.

Dr. Brown had never married, and after the death of his parents he had continued to reside with his brothers and sisters at their home in Germantown. In his prime he was a strikingly handsome man, tall, broad-shouldered and dark-haired. His mind was always

²⁸ "Notes on the Geology of Antigua," *Proc. Acad. Nat. Sci. Phila.*, 1913, pp. 584-616.

²⁹ "Fresh Water Mollusks of the Oligocene of Antigua," *ibid.*, 1914, pp. 209-213.

³⁰ "Oligocene Fossils from the Neighborhood of Cartagena, Colombia, with Notes on Haitian Species," *ibid.*, 1917, pp. 32-41.

active and alert. His eyes would kindle as his interest was aroused in conversation or congenial occupation, and among his intimates his fine sense of humor was constantly in evidence. His powers of observation were keen and his deductions remarkably accurate. He had well-defined opinions on scientific topics and, while not hesitating to express them, he was loath to force them upon others or to engage in argument or controversy, and in assuming without protest whatever tasks were allotted to him he often bore far more than his share of the burdens of life.

His quiet unassuming manner attracted those with whom he came in contact, while he possessed none of the qualities that make enemies.

In his death science loses an investigator and teacher of exceptional ability and this Society an officer noted for his devotion and loyalty.

A long line of students will, in years to come, recall with pleasure their association with Amos Brown at the University—his kindness; his fairness; and his earnestness of purpose. A smaller group of scientific associates will cherish recollections of his reverence for the sciences which he helped to advance and his faithfulness to the trusts that were placed upon him. A still smaller group, who were privileged to know the real man in the intimacy of close companionship, will mourn the loss of that which has been described as the easiest thing to speak of, but the hardest to find—a true friend.

WITMER STONE.

MINUTES.

MINUTES.

Stated Meeting January 4, 1918.

Curator C. L. DOOLITTLE, C.E., Sc.D., LL.D., in the Chair.

The decease was announced of Joseph P. Remington, Ph.D., on January 1, 1918, in his 71st year.

Dr. Witmer Stone read an Obituary Notice of Prof. Amos P. Brown (see page i).

Mr. Edgar L. Hewett read a paper on "Our Cultural Heritage from Ancient America," which was discussed by Dr. Jastrow, Prof. L. W. Miller, Mr. E. S. Balch and Mr. Hewett.

The judges of the Annual Election held this day between the hours of two and five in the afternoon reported that the following named members were elected according to the Laws, Regulations and Ordinances of the Society, to be the Officers for the ensuing year:

President.

William B. Scott.

Vice-Presidents.

Albert A. Michelson,
George Ellery Hale,
Joseph G. Rosengarten.

Secretaries.

I. Minis Hays,
Arthur W. Goodspeed,
Harry F. Keller,
Bradley Moore Davis.

Curators.

Charles L. Doolittle,
William P. Wilson,
Leslie W. Miller.

Treasurer.

Henry La Barre Jayne.

Councillors.

(To serve for three years.)

Bertram B. Boltwood,

Ernest W. Brown,

Francis B. Gummere,

Herbert S. Jennings.

The Finance Committee and the Treasurer presented their annual reports.

Stated Meeting, February 1, 1918.

WILLIAM B. SCOTT, Sc.D., LL.D., President, in the Chair.

Dr. Alonzo E. Taylor, a newly elected member, subscribed the Laws and was admitted into the Society.

The Society commemorated the Centenary of the Death of Caspar Wistar, M.D., and the following papers on Dr. Wistar were read:

"As a Scientist and Philosopher," by Dr. I. Minis Hays.

"As a Human Anatomist," by Dr. George A. Piersol.

"As a Comparative Anatomist," by Prof. William B. Scott.

Stated Meeting, March 1, 1918.

WILLIAM B. SCOTT, Sc.D., LL.D., President, in the Chair.

Mr. Pierre S. duPont, a newly elected member, subscribed the Laws and was admitted into the Society.

The decease was announced of Samuel G. Dixon, M.D., on February 26, 1918, æt. 67.

Prof. Vernon Kellogg read a paper entitled "Behind the German Lines in Belgium and France."

Mr. Benjamin Smith Lyman presented notes on "The Soul," "The Word of God," "Classical Studies," and "Of." (See page 627.)

Stated Meeting, April 5, 1918.

WILLIAM B. SCOTT, Sc.D., LL.D., President, in the Chair.

The decease was announced of John Fulton, at Johnstown, Pa., on January 20, 1916, æt. 89.

Mr. Eli K. Price read a paper on "The Park System of Philadelphia," which was discussed by Prof. Miller, Dr. Keen, Prof. Scott and Mr. Bryant.

Mr. Price, on behalf of the Committee on the Henry M. Phillips Prize, presented the following report:

"The Committee on the Henry M. Phillips Prize have the honor to report that the Judges appointed by the Society to pass on the essays that might be submitted on 'The Relation of the Initiative, Referendum and Recall,' in competition for the Prize, have found to their regret that no essay on the chosen subject has been received of such originality and importance as to justify an award of the Prize."

"The Committee therefore recommend the adoption of the following resolutions:

"*Resolved*, That no award of the Phillips Prize be made in pursuance of the competition invited for the year 1918.

"*Resolved*, That the thanks of the Society be extended to the Hon. Charles Matteson, of Providence, Prof. Charles E. Merriam, of Chicago, Dr. Westel W. Willoughby, of Washington, Prof. Henry J. Ford, of Princeton, and the Hon. Hampton L. Carson, of Philadelphia, for their valuable services as Judges of the competition."

The Report was accepted and the resolutions appended thereto were adopted.

Stated General Meeting, April 18, 19 and 20, 1918.

Thursday Afternoon, April 18, 1918.

Opening Session, 2:30 o'clock.

WILLIAM B. SCOTT, Sc.D., LL.D., President, in the Chair.

The following papers were read:

"Efforts of Food Control under Queen Elizabeth," by Edward P. Cheyney, A.M., LL.D., Professor of European History, University of Pennsylvania.

- "Control of Commerce in War Time," by William E. Lingelbach, Professor of Modern European History, University of Pennsylvania.
- "The Influence of Russian Political Parties on Domestic and International Questions," by Alexander Petrunkevitch, Ph.D., Professor of Zoölogy, Yale University.
- "Problems of War Finance," by Thomas S. Adams, Ph.D., Professor of Political Economy, Yale University.
- "Control of Railroads of the United States," by Emory R. Johnson, Sc.D., Professor of Transportation and Commerce, University of Pennsylvania.
- "The Sanitation of Camps," by Col. Frederick F. Russell, Medical Corps, U. S. A.

Friday, April 19.

Morning Session, 10:30 o'clock.

J. G. ROSENGARTEN, LL.D., Vice-President, in the Chair.

Dr. Frank Dawson Adams, a recently elected member, subscribed the Laws and was admitted into the Society.

The following papers were read:

- "The Art of George Catlin," by Edwin Swift Balch, A.B., of Philadelphia (see p. 144), which was discussed by Dr. Holland.
- "Surgical Shock," by William T. Porter, M.D., LL.D., Professor of Comparative Physiology, Harvard University, which was discussed by Dr. Keen.
- "The Relations of French and American Thought in the 18th and 19th Centuries," by Albert Schinz, A.M., Ph.D., Professor of French Literature, Smith College, Northampton, Mass.
- "Type-writer Keyboards; An Inquiry for Some Rational Ones," by Charles R. Lanman, Ph.D., LL.D., Professor of Sanskrit, Harvard University.
- "Changing of the Sex-Ratio of the Rat," by Helen D. King, Associate Professor of Embryology, Wistar Institute, Philadelphia, which was discussed by Prof. Jennings.

- "History of the Study of Greek Vase Paintings," by Stephen B. Luce, Curator of Greek Antiquities, Museum of the University of Pennsylvania. (See page 649.)
- "The Naiades of the Upper Tennessee Drainage," by Arnold E. Ortmann, Ph.D., Sc.D., Professor of Physical Geography, University of Pittsburgh. (See p. 521.)
- "A New Type of Insect Larva," by William Morton Wheeler, Ph.D., Sc.D., Professor of Economic Entomology, Bussey Institution, Harvard University. (See p. 293.)
- "A Critical Survey of the Sense of Hearing in Fishes," by George H. Parker, Sc.D., Professor of Zoölogy, Harvard University. (See p. 69.)
- "The Perfecting Principle," by L. H. Bailey, LL.D., Late Professor of Horticulture, Cornell University.
- "Medicinal Plants—Present and Future Supplies," by Henry Kraemer, Ph.D., Head of the Dept. of Pharmacology, University of Michigan.
- "Parasitism among the Red Algæ," by William A. Setchell, Ph.D., Professor of Botany, University of California. (See p. 155.)

Afternoon Session, 2 o'clock.

ALBERT A. MICHELSON, Ph.D., Sc.D., LL.D., F.R.S., Vice-President
in the Chair.

The following papers were read:

- I. "Preliminary Notes of Some New Species of Agarics" (see p. 354), and
 - II. "The Genus *Galerula* in North America," by George F. Atkinson, Ph.D., Professor of Botany, Cornell University. (See p. 357.)
- "Temperature, Imbibition and Growth," by D. T. MacDougal, Ph.D., LL.D., Director of the Department of Botanical Research, Carnegie Institution of Washington.
- "Variation in Blueberry Hybrids," by Frederick V. Coville, Curator of the U. S. National Herbarium, Department of

Agriculture, Washington, D. C., which was discussed by Professors Harshberger, Webster, Goodspeed and L. H. Bailey. "Organization, Reproduction and Heredity in *Pediastrum*," by Robert A. Harper, Ph.D., Professor of Botany, Columbia University. (See p. 375.)

I. "Dependence of the Earth's Magnetic State on Solar Conditions 1888-1916," and

II. "The Potentials of Certain Magnetized Bodies," by Louis A. Bauer, Ph.D., Sc.D., Director of the Department of Terrestrial Magnetism, Carnegie Institution of Washington, which were discussed by Professors Webster, and Michelson.

"Development of Magnetic Susceptibility in Manganese Steel by Prolonged Heat Treatment," by Charles Francis Brush, Ph.D., Sc.D., LL.D., of Cleveland (see p. 344), which was discussed by Dr. Bauer.

"Accelerometers," by N. W. Akimoff, of Philadelphia, which was discussed by Dr. Webster.

"Luminescence of Radium Salts," by D. H. Kabakjian, Assistant Professor of Physics, University of Pennsylvania, and E. Karrer, of Philadelphia.

Friday evening, 8:30 o'clock.

Lieut.-Col. Robert Andrews Millikan, Ph.D., Sc.D., spoke on "Science in Relation to the War."

Saturday, April 20.

Executive Session, 9:30 o'clock.

WILLIAM B. SCOTT, Sc.D., LL.D., President, in the Chair.

On the recommendation of the Officers and Council nominations for foreign membership were suspended by unanimous vote until the number of foreign members is reduced to seventy-five.

Prof. Ernest W. Brown, on behalf of the Nominating Committee, recommended that the term of service of the curators, like that of Councillors, be limited to three consecutive years.

On motion this recommendation was unanimously adopted.

Pending nominations for membership were read and the Society proceeded to an election.

The tellers reported that the following nominees had been elected to membership:

Residents of the United States.

Henry Andrews Bumstead, A.B., Ph.D., New Haven.

Philip Powell Calvert, Ph.D., Philadelphia.

Clarence Griffin Child, Ph.D., L.H.D., Philadelphia.

William T. Councilman, A.M., M.D., LL.D., Boston.

Victor George Heiser, M.D., New York.

Herbert C. Hoover, B.A., LL.D., Washington.

Aleš Hrdlička, M.D., Washington.

Gilbert Newton Lewis, A.M., Ph.D., Berkeley.

Theodore Lyman, Ph.D., Cambridge.

J. Percy Moore, Media, Pa.

Louis Valentine Pirsson, M.A., New Haven.

George Harrison Shull, B.S., Ph.D., Princeton.

Joseph Swain, B.L., M.S., LL.D., Swarthmore.

William Roscoe Thayer, A.M., LL.D., Litt.D., L.B.H., Cambridge.

Samuel Wendell Williston, A.M., M.D., Ph.D., Sc.D., Chicago.

Foreign Residents.

Joseph Jacques Cesaire Joffre, Paris.

Paul Painlevé, Paris.

Raymond Poincaré, Paris.

Morning Session, 10 o'clock.

WILLIAM B. SCOTT, Sc.D., LL.D., President, in the Chair.

Mr. William Roscoe Thayer, a newly elected member, subscribed the Laws and was admitted into the Society.

The following papers were read:

"Motions in the Stellar Systems Struve 1836 and Struve 208,"
by Eric Doolittle, Professor of Astronomy, University of
Pennsylvania.

"The Number of the Spiral Nebulæ," by H. D. Curtis, As-

tronomer, Lick Observatory, Mt. Hamilton, Cal. (see p. 513), which was discussed by Prof. E. W. Brown.

"Italy in the Triple Alliance," by William Roscoe Thayer, Litt.D., L.H.D., LL.D., Cambridge, Mass.

"Ballistic Experiments by a New (?) Method," by Arthur Gordon Webster, Sc.D., LL.D., Professor of Physics, Clark University, Worcester, and Mildred Allen.

"Some Considerations on the Ballistics of a Gun of Seventy-five Miles Range," by Arthur Gordon Webster, Sc.D., LL.D., Professor of Physics, Clark University, Worcester, Mass.

"The Relation of Deposits of Iron and Coal to the Great War," by William H. Hobbs, Ph.D., Sc.D., Professor of Geology, University of Michigan.

"The Peculiar Geographical Features of Northwestern France and their Bearing on the War," by William Morris Davis, Sc.D., Ph.D., Professor Emeritus of Geology, Harvard University.

"Rig-Veda Repetitions," by Maurice Bloomfield, Ph.D., LL.D., Professor of Sanskrit and Comparative Philology, Johns Hopkins University.

Afternoon Session, 2 o'clock.

WILLIAM B. SCOTT, Sc.D., LL.D., President, in the Chair.

The following papers were read:

"The Babylonian Origin of the Jewish Method of Slaughter," by Paul Haupt, Ph.D., LL.D., Professor of Semitic Languages, Johns Hopkins University.

"Soldiers' and Sailors' Insurance," by Samuel McCune Lindsay, Ph.D., LL.D., Professor of Social Legislation, Columbia University, New York. (See page 632.)

Symposium on Food Problems in Relation to the War—

"Physiological Effects of Prolonged Reduced Diet on Twenty-five Men," by Francis G. Benedict, Ph.D., Sc.D., Director of the Nutrition Laboratory of the Carnegie Institution of Washington. (See p. 479.)

"Food Conservation from the Standpoint of the Chemistry of Nutrition," by Henry C. Sherman, Ph.D., Professor of Food

- Chemistry, Columbia University, New York. (See p. 491.)
- "Some Economic Aspects of the American Food Supply," by J. Russell Smith, Ph.D., Professor of Industry, Wharton School of Finance and Commerce, University of Pennsylvania. (See p. 501.)
- "Food Control and Conservation in the United States Army," by John R. Murlin, Major, Sanitary Corps, U. S. A.

Stated Meeting, May 3, 1918.

WILLIAM B. SCOTT, Sc.D., LL.D., President, in the Chair.

Dr. Philip P. Calvert, a newly elected member, subscribed the Laws and was admitted into the Society.

Acknowledgments of election were received from

Philip Powell Calvert, Ph.D.
 William T. Councilman, A.M., M.D., LL.D.
 Victor George Heiser, M.D.
 Herbert C. Hoover, B.A., LL.D.
 Aleš Hrdlička, M.D., Washington.
 J. Percy Moore.
 Louis Valentine Pirsson, M.A.
 George Harrison Shull, B.S., Ph.D.
 Joseph Swain, B.L., M.S., LL.D.
 William Roscoe Thayer, A.M., LL.D., Litt.D., L.H.D.
 Samuel Wendell Williston, A.M., M.D., Ph.D., Sc.D.

The following papers were read:

"Inorganic Evolution from the Astronomic and Atomic Aspects," by Eric Doolittle, C.E., and Arthur W. Goodspeed, Ph.D., which were discussed by Professor Snyder, President Scott, Mr. Willcox, and Dr. Keen.

Stated Meeting, November 1, 1918.

WILLIAM B. SCOTT, D.Sc., LL.D., President, in the Chair.

Professor J. Percy Moore and President Joseph Swain, newly-elected members, subscribed the Laws and were admitted into the Society.

Letters accepting membership were received from
His Excellency Raymond Poincaré,
Le Maréchal Joseph Joffre and
Prof. H. A. Bumstead

and a declination from Prof. Clarence G. Child.

A communication from the Rector of the University of Lund stating that the University would celebrate on the 27th of September of this year, the 250th Anniversary of its founding was read. The Secretaries were instructed to send to the University the congratulations and good wishes of the Society on the occasion.

The decease was announced of

Prof. Guido Cora, at Piedmont, on October 10, 1917, æt. 66.

Grove K. Gilbert, A.B., A.M., LL.D., at Jackson, Mich., on
May 1, 1918, æt. 75.

Frank Miles Day, B.S., M.A., at Philadelphia, on June 15, 1918,
æt. 57.

Rt. Rev. John J. Keane, at Dubuque, Iowa, on June 22, 1918,
æt. 79.

James Douglas, B.A., LL.D., at New York, on June 25, 1918,
æt. 81.

Stephen Farnum Peckham, A.M., on July 11, 1918, æt. 79.

William H. Greene, M.D., at Wenonah, N. J., on August 8,
1918, æt. 65.

Maxime Bôcher, A.B., Ph.D., at Cambridge, Mass., on Sep-
tember 12, 1918, æt. 51.

Mr. Joseph Willcox, at Philadelphia, on October 1, 1918, æt. 89.

Dr. Isaac Norris, at Florence, Italy, on October 22, 1918, æt. 84.

Prof. John A. Miller read a paper on "The Total Solar Eclipse
of June 8, 1918," which was discussed by Prof. Snyder.

Special Meeting, November 21, 1918.

WILLIAM B. SCOTT, D.Sc., LL.D., President in the Chair.

DR. ETIENNE BURNET, of the French Educational Mission to
the United States, read a paper on "Pasteur as a Representative of
the French Scientific Spirit."

Stated Meeting, December 6, 1918.

WILLIAM B. SCOTT, D.Sc., LL.D., President in the Chair.

Letters accepting election to membership were read from

Gilbert Newton Lewis, A.M., Ph.D.

Theodore Lyman, Ph.D.

The decease was announced of,

George Francis Atkinson, Ph.D., at Tacoma, on November 14th,
1918, æt. 65.

Charles Richard Van Hise, M.S., LL.D., at Milwaukee, on
November 19th, 1918, æt. 61.

Samuel A. Green, M.D., at Boston, on December 5th, 1918,
æt. 88.

Prof. Franklin Edgerton read a paper on "India's Place in the
Modern World," which was discussed by Dr. Keen, Prof. R. G.
Kent, Mr. Bryant, President Scott and Prof. Edgerton.

The President delivered his Annual Address.

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MAGELLANIC PREMIUM

FOUNDED IN 1786 BY JOHN HYACINTH DE MAGELLAN, OF LONDON

1919

THE AMERICAN PHILOSOPHICAL SOCIETY

HELD AT PHILADELPHIA, FOR PROMOTING USEFUL KNOWLEDGE

ANNOUNCES THAT IN

DECEMBER, 1919

IT WILL AWARD ITS

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